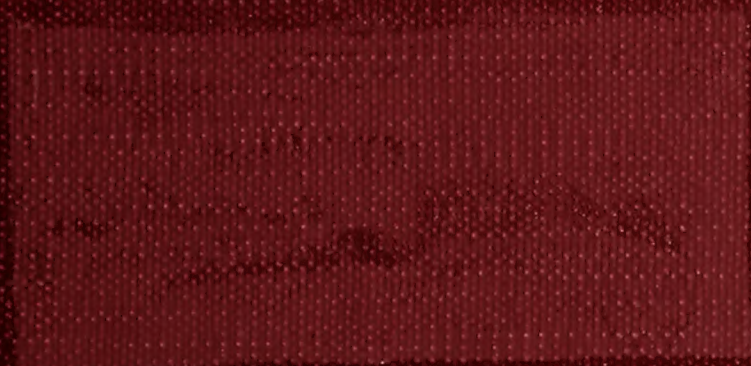
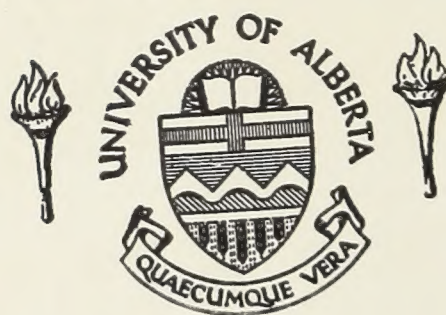




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THE UNIVERSITY OF ALBERTA
THE MORPHOLOGY AND FUNCTION OF THE MOUTHPARTS
OF MOSQUITO LARVAE
A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
OF MASTER OF SCIENCE

BY

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EDMONTON, ALBERTA

SEPTEMBER, 1962



ABSTRACT

The structure and function of the mouthparts of mosquito larvae were studied. Emphasis was placed on the study of the controversial homologies of parts of the maxilla and the labium. The name cardobasistipes is proposed for the triangular sclerite posterior to the base of the maxilla, previously known as the cardo or the palpifer. The numbers of serrations on the plates of the prementum and the submentum were found to be of taxonomic value. The mechanism of movement of the hairs of the labral brushes was elucidated, central movement is muscled, lateral return is by elasticity. Various degrees of flexibility of the cuticle of the mouthparts were found by staining with Mallory's triple stain. This variation was confirmed by observing the mouthparts of several species in action. The serrated tips of the labral brush hairs, present in most of the browsing species of Aedes and Culiseta that were studied, are flexible in spite of their function which is raking of food particles from surfaces.

Other larvae, Culex territans, Culiseta morsitans, whose labral brushes consist of long, simple hairs, do not browse, but filter out food from the water which is brought to the mouth by the labral brush current. Since the size range of food particles found in the guts of these larvae was similar to the size range of the spaces between the labral brush hairs, it is correct to refer to these larvae as filter feeders. After browsing larvae were kept in a suspension of charcoal in water, the particles from their guts were measured and were compared with the dimensions of the natural food particles. The particles of charcoal were smaller than those of the natural food in larvae of the same species. The filter feeding mechanism was employed by the browsers in the suspension of charcoal in water. No selection in the type of natural food ingested was found among the browsing and filter feeding larvae.

The morphology of the mouthparts of the larvae of Aedes canadensis and A. cinereus was found to be intermediate between those of the typical filter feeding and typical browsing species. Both filter feeding and browsing were observed in each species.

The feeding behavior of the predatory larvae of Chaoborus and Mochlonyx was observed. Cannibalism was observed among the larvae of M. velutinus.

ACKNOWLEDGEMENTS

I wish to express my gratitude to Professor B. Hocking for stimulating my interest in the study of mosquitoes, and for helping me choose the problem of this investigation. To Professor Hocking and Dr. Janet Sharplin (nee Petersen) I am indebted for many suggestions and criticisms during the course of the work, and for reading and correcting the manuscript. I am grateful to Dr. W. G. Evans, Dr. G. E. Ball, and fellow graduate students, Department of Entomology, for valuable discussions. Dr. Lorene Kennedy, Department of Botany, has identified the intestinal contents of many mosquito larvae. Miss J. C. Shore and Miss A. Zalums, Department of Entomology, have offered many services.

My thanks are due to Dr. J. McLintock, Canada Department of Agriculture, Ottawa, and Mr. J. A. Shemanchuk, Department of Agriculture, Lethbridge, for providing me with eggs of Culiseta inornata, and to Professor J. G. Rempel, Department of Biology, University of Saskatchewan, Saskatoon, for series of larvae of Culex species.

I wish to thank the following translators, all of whom are from the University of Alberta: Rev. Brother Bonaventure, Department of History, for translating Latin; Dr. K. Westerskov, Department of Zoology, for translating Danish; and the following persons for translating German: Rev. G. Seifert, School of Physical Education, Miss Claudia Ritzel, Faculty of Medicine, and Mr. L. Sutton, Department of Zoology. Mrs. E. Ilchuk of Sherwood Park, Alberta, has typed most of the manuscript. Miss S. Mooney, reference librarian, University of Alberta, has obtained many publications by interlibrary loans.

Finally, I express my grateful thanks to the Canada Defence Research Board for financial assistance.

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1.0 LITERATURE REVIEW

1.1. HISTORICAL

1.1.1. Pre-Linnaean Period.

In early English scientific literature mosquitoes are referred to as gnats, and in Latin as culex. Mouffet (1634) states that observations about culex date back to Aristotle (388 - 322 B.C.) who was not certain whether culex were generated by other culex, but thought that possibly regeneration occurred by means of a "worm" as in the flies. However, Aristotle and his followers believed in the spontaneous generation of insects, and it was only in the seventeenth century that the simple experiments of F. Redi (1626 - 97) conclusively disproved this theory (Busvine 1951). Mouffet also credits Pliny (23 - 79 A.D.) and Albertus Magnus (1206 - 80) with observations on culex. It is not certain, though, whether Pliny recorded his observations on mosquitoes or on some other insects. Bostock's and Riley's translation of The Natural History of Pliny refers to swarms of "gnats" above a fig tree and states that these "gnats" are born by the fig tree. A footnote says that these "gnats" may be Cantharides. However, from the description of the habits of those insects it seems almost certain that they were Agaontids (Hocking, pers comm.).

Hooke (1664) presents a rather good drawing of a mosquito larva, but he does not interpret all the parts of its anatomy accurately; for example, he states that the anus is in the respiratory siphon. He further states the following of the "Water-Insect or Gnat": "... It is suppos'd by some, to deduce its first origin from the putrifaction of Rain Water..." Hooke also writes that the larvae can move gently through the water by moving their mouthparts, and "eat" their way up through the water.

Reaumur (1738) describes and illustrates the external features of a mosquito larva which seems to be a Culex species (according to Shannon (1931), Culex pipiens). He gives a very good description of the workings of the labral brushes which he calls crescents (croissans). He states that these crescents produce a current which is directed towards the mouth and brings to the larva the food which it needs, such as ... "imperceptible insects, small plants, and perhaps small pieces of earth which are found in the water..." He also describes the browsing activity of a larva. Meinert (1886) and Raschke (1887) besides mentioning the work of Hooke and Reaumur list the following persons who have contributed to the descriptions of Culex larvae: Swammerdam, Reviglias, de San Gallo, and Haller.

1.1.2. Post-Linnaean Period

Linnaeus (1758) published descriptions of some species of Culex. Meinert (1886) also states that in 1746 Linnaeus distinguished Culex pipiens and Culex biforcatus, and the latter species was later renamed as a species of Anopheles by Meigen. Meinert (1886) reviews the works of students of mosquitoes of the early post-Linnaean period. According to him, the following workers had made important contributions to the knowledge of mosquitoes: Joblot, Geoffroy, Slabber, Kleemann, and Gilchrist. He states that the last two men mentioned here had observed the function of labral brushes of mosquito larvae.

From the literature it seems that not much detailed attention was paid to mosquitoes until it was proved that these insects had the ability to spread certain diseases of man. In 1878 Patrick Manson (Manson and Cobbold 1879, Ross 1930), working in China, described the development of the nematode worm Wuchereria bancrofti Cobbold in the body of a mosquito.

Later, with other workers he incriminated the mosquito in spreading filariasis (Busvine (1951). Ronald Ross (Ross 1923, Busvine 1951) discovered malarial parasites in a species of an Anopheles mosquito in 1897. The Italian workers Bastianelli, Bignami, Celli, and Grassi added to the knowledge of malaria transmission, and final proof came from the experiments of Sambon and Low in the Italian Campagna (Ross 1923, Busvine 1951).

Before knowing definitely that insects could transmit diseases, the attitude of entomologists toward the study of insects that affect man and domestic animals is expressed by Goreau(1866) thus:

"These insects have received less attention than those which affect our cultivated plants; but this is perfectly natural, because, as a general rule however troublesome they may be, the injury which they do us is of far less importance."

The same author described characters and habits of Culex pipiens, other species of Culex, and Anopheles maculipennis. White (1883) studied the histological development of the larva of Corethra plumicornis. The development of Culex pipiens was also studied by an anonymous author in 1885. The best known studies on mosquito larvae in the 19th century are those of Meinert (1886) and Raschke (1887). Larval morphology, function of mouthparts, and some aspects of larval and adult habits are discussed by these authors. Reviews of previous works on mosquitoes are also included in each work.

Towards the close of the 19th century the mouthparts of a number of insects were studied by the following authors: Lowne (1873) - the structure of mouths in insects; Meinert (1880, 1881) the mouthparts of various insects including Diptera; Dimmock (1881) - the sucking apparatus of Diptera, including Culex; Becher (1882) - mouthparts of various Diptera; Dewitz (1882) - analogies and homologies of mouth-

parts of various insects; Chatin (1884) - mouthparts of mandibulate insects; Macloskie (1885) - larval Musca; Plateau (1885) - morphology and function of the mouthparts of Coleoptera; Smith (1890) - the mouthparts of Diptera. Brauer (1884) classified Diptera with the help of larval head characters.

In this century some of the important contributions to the understanding of the insect head and mouthparts were made by the following authors, aside from the ones listed in Table 1.: Dyar (1902) larvae of North American Culicidae; Wesche (1903) - the labial and maxillary palpi in Diptera; Christophers (1906), Hosford (1913) - insect cranium, Nininger (1915) - mouthparts of Orthoptera; Crampton (1921, 1923, 1932) - comparisons and phylogeny of insect head and mouthparts; Gahan (1921); McGillivray (1924) - labium of certain Holometabola; Das (1937) - structure of insect larvae; Vargas (1940) - maxillary index in American Anopheles; Ferris (1943, 1947, 1948) - insect morphology; Snodgrass (1935, 1944, 1947, 1958) - morphology of insects; Cook (1944, 1947) - Dipteran larvae, morphology and evolution; Matheson (1944, 1950) - mosquitoes and medical importance; Rozeboom and Komp (1950) - Culex spp. review; Chiswell (1955) - Tipula larva; Butt (1957, 1958) - Embryology; DuPorte (1958) - preoral structures in insects.

1.2. MORPHOLOGY AND FUNCTION OF THE MOUTHPARTS OF MOSQUITO LARVAE

1.2.1. Introduction.

The names used by various authors for the mouthparts of mosquito larvae are summarized in Table 1. From this it is evident that there is disagreement among the various authors on the homology of

Table 1. Summary of names used for mouthparts and some cranial sclerites of mosquito larvae, (a) to 1905.

AUTHOR	LABRAL AREA						
1. Present work <u>Aedes</u> , <u>Culex</u> , <u>Culiseta</u>	fronto- clypeus	labrum	lateral labral brush	median labral brush	posterior tormal apodeme	trans- verse bar	epipha- ryngeal bar
2. Meinert 1886 <u>C. annulatus</u>	scutum of 3rd meta- mere	clypeus	whirl- ing organ	scutum of 1st meta- mere			
3. Raschke 1887 <u>C. nemorosus</u>		upper- lip	strudel apparat				
4. Miall 1895 <u>Corethra</u>		labrum					
5. Giles 1901 <u>A. rossii</u> , <u>C. fat-</u> <u>ignas</u> , <u>Mochlonyx</u> <u>Chaoborus</u>	clypeus	labrum	whorl organ				
6. Theobald 1901 - 1907 <u>Anopheles</u> , <u>Megarhinus</u>			whorl organ brush				
7. Nuttall & Shipley 1902 <u>Anopheles</u>		clypeus	brush				
8. Johanssen 1903 <u>Culex</u> , <u>Psorophora</u> <u>Aedes</u> , <u>Corethra</u>		clypeus					
9. Thompson 1905 <u>Culex</u>	rostrum		flab- ella	pala- tum	flabellar inner refractor insertion		epipha- ryn- x

Table 1 (a) continued

	M A X I L L A			L A B I U M			CRANIAL WALL		
	MANDIBLE	palp	disti- stipes	cardo- disti- stipes	pre- mentum	sub- mentum	au- laeum	sub- gena	post- gena
1.	mandible	palp	lacinia	inter- nal	disti- stipes	ex- ternal	lobe		
2.	mandible	palp	lobe						
3.									
4.	mandible	palp	maxilla					under- lip	
5.	mandible	palp	maxilla					labium	
6.	mandible	palp	maxilla					lower lip	
7.	mandible	palp	maxilla					labial plate	
8.	mandible	palp	maxilla					lower lip	
9.	mandible	palp	maxilla					labium	
	mandible	palp	maxilla					hypo- pharynx labium	mental sclerite

Table 1. Summary of names used for mouthparts and some cranial sclerites of mosquito larvae, (b) 1906 to 1938.

AUTHOR	L A B R A L A R E A					
Present work <u>Aedes, Culex,</u> <u>Culiseta</u>	fronto- clypeus	labrum	lateral labral brush	median labral brush	posterior tormal apodeme	Epipha- ryngeal bar
10. Mitchell 1906 <u>Anopheles, Cu-</u> <u>lex, Psorophora</u>			mouth brush			
11. Imms 1907 & 1908 <u>Anopheles</u>		clypeus	brush		chitinous apodeme of epipharynx	epipha- ryn
12. Wesche 1910 <u>Culex</u>		clypeus	brush			
13. Howard, Dyar, & Knab 1912 <u>Aedes, Culex</u>	rostrum	labrum	mouth brush flabella	pala- tum		epipha- ryn
14. Wesenberg-Lund 1921 <u>Culiseta</u> <u>Aedes, Culex</u>		labrum	flabella	pala- tum	apodeme	
15. Salem 1931 <u>Aedes fas-</u> <u>ciatus</u>		labrum	feeding brush	pala- tum	apodeme	clypeo- labral suture epipha- ryn
16. Bekker 1938 <u>Anopheles</u>		clypeus	flabella	antero- median lobe	longi- tudinal lever	trans- verse girdle epipha- ryn
17. Marshall 1938 <u>Anopheles</u> <u>Culex</u>	fronto- clypeus	pre- clypeus	mouth brush	labrum		epipha- ryn 15.

Table 1 (b) continued

MANDIBLE	M A X I L L A			L A B I U M			CRANIAL WALL		
	palp	lacinia	disti- stipes	cardo- disti- stipes	pre- mentum	sub- mentum	au- laeum	sub- gena	post- gena
10.	mandible	palp	lacinia	disti- stipes	cardo- disti- stipes	pre- mentum	sub- mentum	au- laeum	sub- gena
11.	mandible	palpus	maxilla						
12.	mandible	palp	maxilla			hypo- pharynx	labial plate		
13.	mandible	palp	maxilla			labium (pre- mentum)	lower lip		
14.	mandible	palp	maxilla			labium hypo- pharynx	hair mental sclerite plate		
15.	mandible	palp	maxilla			labium & hypo- pharynx	hair mental sclerite plate		
16.	mandible	palp	maxilla			labium	sub- mentum		
17.	mandible	palp	maxilla			labium			
	mandible	palp	maxilla			hypo- pharynx	sub- mentum		

Table 1. Summary of names used for mouthparts
and some cranial sclerites of mosquito larvae, (c) 1944 to 1952.

AUTHOR	L A B R A L A R E A						
Present work <u>Aedes, Culex,</u> <u>Culiseta</u>	fronto- clypeus	labrum	lateral labral brush	median labral brush	posterior tormal apodeme	trans- verse bar	epipha- ryngeal bar
18. Cook 1944&49 <u>Culiseta</u> <u>incidens</u>	clypeus	labrum	labral brush	pala- tum	mes- sorial apodeme		palatal bar
19. Matheson 1944 <u>Anopheles</u>	clypeus	labrum	mouth brush	pala- tum			
20. Montchadsky 1945 <u>Chaoborus</u>							
21. Farnsworth 1947 <u>A. quadrimaculatus</u>	clypeus	labrum	labral brush	median labral brush	messorial apodeme		palatal bar
22. Schremmer 1949 <u>A. maculipennis</u>	fronto- clypeus	labrum					epipharynx apparatus
23. Chaudonneret 1951 <u>C. pipiens</u>	clypeus	labrum		labrum	messorial		epipharynx
24. Foote 1952 <u>C. (M.) peccator</u> <u>C. (M.) atratus</u>	clypeus	labrum	mouth brush	mouth brush	messorial		palatal bar

Table 1 (c) continued

MANDIBLE	M A X I L L A			L A B I U M		CRANIAL WALL			
			disti-	cardo-					
	mandible	palp	lacinia	stipes	pre- mentum	sub- mentum	au- laeum	sub- gena	post- gena
18.									
	mandible	palp	stipes	palp- ifer	pre- mentum	sub- mentum	au- laeum	maxillary segment	
19.									
	mandible	palp	maxilla		pre- mentum	mentum			
20.									
	mandible	palp	maxilla						
21.					hypophar- yngeal body	inner tooth of mentum	outer tooth of mentum	maxillary plate	
22.									
	mandible	palp	maxilla			labium			
23.									
	mandible	palp	maxilla						

Table 1. Summary of names used for mouthparts
and some cranial sclerites of mosquito larvae, (d) 1956 to 1960.

AUTHOR	L	A	B	R	A	L	A	R	E	A
Present work						lateral	median			
Aedes, <u>Culex</u> , <u>Culiseta</u>	fronto- clypeus	labrum				labral brush	labral brush	torma	posterior tormal apodeme	trans- verse bar
25. Cook 1956										
Chaoborus,										
Mochlonyx, Eucoethra	clypeus	labrum								
26. Shalaby 1957										
Ae: aegypti, Psorophora C. fasciatus	frons	pre- clypeus				lateral labral brush	pala- tum	labral brush apodeme	post apod.	trans- verse bar
27. Menees 1958										
Anoph: quadri- maculatus	* A-clypeus P-frons	labrum				mouth brush	median brush	torma	anterior interior- mal bar	epipha- ryngeal sclerite
28. Snodgrass 1959										
Aedes; <u>Culex</u> , <u>Culiseta</u> , <u>Anopheles</u>	fronto- clypeus	labrum				lateral feeding brush	median brush	torma	apodeme	epipha- aryngeal bar
29. Surtees 1959										
African spp. of <u>Culex</u> , <u>Aedes</u>						mouth brush				
30. Christophers 1960										
Ae. aegypti	A.-clypeus P-frons	pre- clypeus				flabel- lum	pala- tum	apodeme	stirrup apodeme	post palatal bar
										epiph a- ryn timer

* A - anterior, P - posterior

Table 1 (d) continued

MANDIBLE	M A X I L L A	L A B I U M	CRANIAL WALL
	cardo disti- stipes	pre- mentum	sub- gena
mandible palp	lacinia stipes	mentum	post- gena
24.			
mandible palp	maxilla	pre- mentum	au- laeum
25.			
mandible palp	stipes	pre- mentum	maxillary plate
26.			
mandible palp	lacinia cardo-stipes	hypo- pharynx	para- glossa
		labio-hypo- pharyngeal	inner tooth of
27.		body	mentum
mandible palp	stipes	labium- hypo- pharynx	outer tooth of mentum
28.			
mandible palp	stipes	labium- hypo- pharynx	post- gena
29.			
mandible palp	maxilla	mentum	
30.			
mandible palp	distal part of maxilla	labium- hypo- pharynx	mental sclerite
			labial area

certain parts. There is less disagreement on the function of these parts, but this aspect of the problem has not been exhausted.

1.2.2. The Labrum

The labrum consists of a small transverse sclerite on the dorsal wall of the head before the clypeus, and a larger membranous undersurface that bears laterally the two vibratory feeding brushes and a median brush. The lateral brushes of the labrum are the organs by which those larvae that feed on particles create currents in the water directed toward the head, and drive a stream of water back to the mouth along the epipharyngeal surface. In many species the individual hairs of the median parts of the brushes are finely pectinate and serve also as combs for retaining particles filtered from the water.

The vibratory movement of the brushes is produced by a pair of strongly muscled sclerites on the under side of the labrum. These sclerites are known as tormae, brush apodemes, and messorae (Table 1). They serve as muscle attachments for the labral muscles. The labrum is operated by four muscles, one pair dorsal, the other ventral, all of which arise on the fronto-clypeus. These muscles insert on a posterior-dorsal apodeme of the torma. Contraction of the muscles evidently rocks the torma mesally on its articular points and thus gives a backward and mesal stroke to the connected brush. The reverse movement of the lateral labral brush, as several writers have noted, results from the elasticity of its basal connections. The following are some of the works in which the musculature of the mosquito larval labrum and of the other mouthparts is fully or partially described: Meinert (1886), Raschke (1887), Thompson (1905),

Imms (1907, 1908), Bekker (1938 a & b), and others (Table 1). A description of the labral brush sclerites and hairs is included in the work of Salem (1931). He states that the chitin of the hair-bearing sclerite of the labral brush "exhibits a peculiar striated appearance." It seems certain that Salem is referring to the sclerotized bars to which the hairs are attached. Christophers (1960) calls these structures by the term "cross bars". In this work the same nomenclature is used for these structures.

In the larvae of Lutzia halifaxi Theobald the membrane at the base of the labral brush is described by Cook (1944 b) as a "penicular area beset with small oval pits arranged in definite rows." Christophers (1960) refers to this membrane as the tessellated membrane in A. aegypti. This nomenclature is followed in the present work. Further information about this structure is given in Section 2.3.2. Shalaby (1956, 1957) described in detail the different hairs of the labral brushes and associated sclerites in the larvae of the following species: Anopheles quadrimaculatus, Aedes aegypti, Culex molestus, and Psorophora ciliata. But none of these authors have *fully* explained the mechanism of movement of the labral brush hairs.

The labral brushes by their movements provide a means of locomotion and a feeding current for the larvae (Wesenberg-Lund 1921, Hocking 1953). Most authors mention only the feeding function of the brushes. Wesenberg-Lund ascribes another function to the brushes; he considers them as the organs which renovate the water in the surroundings of the larvae.

1.2.3. The Preoral Cavity

Snodgrass (1959) describes the preoral cavity as follows: "The undersurface of the labrum is continuous with the so-called epipharyngeal surface below the clypeal region, which extends back to the mouth. In most adult insects the part of the preoral cavity above the base of the hypopharynx becomes a special food pocket, the cibarium, opening directly into the mouth. In the mosquito larva the shortness of both the labium and the hypopharynx leaves the entire preoral cavity open below, but still it serves as a channel for water carrying food particles to the mouth. In the tipulid larva, however, there is a short cibarial pocket above the hypopharyngiolabial

lobe just in front of the mouth. In the adult mosquito and other sucking insects the closed cibarium becomes a preoral sucking pump. In the mosquito larva the pharynx assumes the sucking function."

1.2.4. The Epipharyngeal Apparatus

The epipharyngeal apparatus which lies between the posterior ends of the tormae is a structure that serves to comb food particles from brushes on the mandibles. Schremmer (1949) called it the Epipharynx-apparat because it is muscled, and it functions actively instead of passively. Palatal bar, epipharynx, and epipharyngeal armature are other names for the structure. It includes a transverse bar which is usually bow-shaped (in the culicines) or V-shaped (in the anophelines) with the arms diverging forward to the posterior ends of the labral tormae. Groups of setae and other structures arise in front of the bar. Shalaby (1957) and Snodgrass (1959) describe the epipharyngeal apparatus in Aedes where it is relatively simple. The bar is slender, gently curved forward, and its ends are connected with the tormal apodemes. Arising in front of the bar are two large brushes of stiff hairs that converge posteriorly beneath the bar. At the sides of the brushes arise a pair of large, tapering, hair-bearing processes directed posteriorly, and at the base of each are found two small clawlike structures.

1.2.5. The mandibles

The mandibles and the maxillae lie on the ventral side of the head, and they are located obliquely in the membrane that turns upward from the submental margins of the postgenae to the hypopharyngeal bars. The mandibles are above the maxillae, and each consists of a flattened lobe with its mesal ends produced into strongly sclero-

tized toothed processes and a lower seta-bearing lobe. Comb-like fringes of long mesally-directed setae arise from the dorsal mandibular margins. When the mandibles are closed their tips do not meet, but come to rest against the prementum. Anteriorly the mandibles articulate at a point which articulates with a process of the postgenal margin just laterad of the maxilla. Strong abductor and adductor muscles move the mandibles in a transverse plane. The principal function of the mandibles of browsing larvae is to collect, by means of their setal combs, food particles from the labral brushes; the incisor points break up larger particles that collect on the prementum. Good descriptions of larval mandibles of various mosquitoes and other Nematocera can be found in the works of Meinert (1886), Raschke (1887) Johannsen (1903), Mitchell (1906), Theobald (1901 to 1910), Wesenberg-Lund (1921), Puri (1925), Farnsworth (1947), Shalaby (1957 a, b, c, d), and many others.

1. 2. 6. The Maxillae

The maxillae are borne on the transverse ventral margins of the postgenae at the sides of the submentum, where they lie below the mandibles. They are so greatly simplified that they have lost the appearance and structure of an ordinary insect maxilla. As can be seen from Table 1, no homologizing of the different parts of the maxilla was attempted until a comparatively recent time. The principal part of each maxilla consists of a flat lobe of rectangular shape with the corners rounded and with inward depressions on the dorsal and ventral sides. Dorsally on the apex it bears a brush of long setae that collect food particles from the labral brushes; on the median side it bears short setae which help to hold food particles and prevent them from moving posteriorly. This rectangular lobe is termed *stipes* by Cook (1944, 1949),

Farnsworth (1947), and by Snodgrass (1959). All these three authors state that the stipes may include the fusion products of the lacinia and the galea. Cook (1944 b) first suggested this, and he got the idea after examining figures of Culicid larval maxillae in the work of Howard, Dyar, and Knab (1912). The stipes is attached to the cranial wall ventrally, and to the submentum medially, and it is activated by two muscles which originate on the cranial wall. According to Cook (1944 b) and Farnsworth (1947), the cranial flexor of the stipes originates on the latero-ventral portion of the ocular lobe (Fig. 2 (b)), and the other maxillary muscle originates mesad to the posterior tentorial pit. Laterad of the stipes is a much narrower cylindrical lobe, thought to be homologous with the palpus by all the authors whose works were reviewed. At the base of the palpus is a small sclerite in the articular membrane, and this sclerite is regarded as the palpifer by most authors except Salem (1931), who considers it as the first segment of the palp, and Snodgrass (1959), who suggests that this may be the cardo.

Authors who have studied mosquito larvae in recent years do not agree on the homologies of the parts of the maxilla (Table-1.). The maxillae of the chaoborine larvae as described by Montchadsky (1937), Schremmer (1949), and Cook (1956) are much more reduced than the maxillae of Aedes or Anopheles.

1. 2. 7. The Labium and Hypopharynx

As can be seen from Table 1, the earlier students of mosquito larvae, aside from naming the triangular serrated sclerotized plate below the larval mouth opening as a lower lip, mentum, or submentum, did not attempt much homologizing with the labium of a generalized insect. Miall and Hammond (1900) are quoted by Shalaby (1956) and other authors as having said that the larva of Chironomus had

lost so many of the original parts of the labium that this single plate was the only labial remnant. Miall and Hammond (1891) state that the labium in Chironomus represents the second pair of maxillae, and that the sclerotized plate seems to correspond more closely with the submentum of orthopterous insects than with the mentum. Wesche (1910), working on Culex larvae, called the serrated plate the lower lip (Figs. 2, 3 (a), sm.) , but considered the softer part above this plate as the labium (Figs. 11, 12). The same view is held by Snodgrass (1959), only he names the serrated plate a hypostomium, and considers it as a part of the subgena. Gouin (1958), working on Chironomus, considers the serrated plate as a part of the subgena, but calls it hypochilum. Salem (1931) considers the serrated plate as homologous with the submentum, but he feels that he should not change its name because it had been known as the mentum for a long time. The fringed plate just below the sclerotized one had hitherto been unnamed, hence Salem proposed to call it the submentum. Cook (1944 b) studied the labium-hypopharynx complex in various culicid larvae, and decided that the serrated plate is homologous with the submentum, and that the area consisting of spines and sclerotized structures just above the submentum is the prementum. The salivary duct opens dorsad of the prementum, and the area dorsal of the salivary duct he considered to be the hypopharynx. Cook (1944 b) introduced a new term , aulaeum, for the fringed plate below the submentum which he considered as a part of the same structure. Aulaeum in Latin means a canopy.

The cranial wall on the ventral surface of the head is called the maxillary plate by Cook (1944 b , 1949). Studying the larva of Anopheles quadrimaculatus, Farnsworth (1947) named the serrated plate the ~~mentum~~, and the lobe below it the submentum. Shalaby

(1957 d) further confused the interpretation of these parts by naming the medial ventral head sclerite as the labial submentum and mentum, the serrated triangular part as the paraglossa, and the fringed lobe the hypopharynx. Comparative studies do not give a basis for this interpretation, but this will be discussed later. Other authors who have attempted to homologize the parts of the labium and the hypopharynx are Menees (1958 a) , Snodgrass (1959), and Christophers (1960) (Table 1).

1. 2. 8. The Pharynx

The pharynx of larvae that feed on water-borne particles is a small, flattened, ovate, or heart - shaped, thin-walled sac opening directly from the wide mouth and tilted upward and posteriorly in the head. From its posterior ventral surface is continued the thick-walled esophagus. The lateral margins of the pharynx are strengthened by two narrow, concentric, rib-like thickenings on each side, convergent to the narrowed posterior end.

" Internally each of these ribs bears a long brush of fine hairs suggestive of the brushes in the mouth of a baleen whale, and in fact they serve the same purpose, namely that of filtering the food matter from the ingested water. " (Snodgrass 1959).

1. 3. CLASSIFICATION OF MOSQUITO LARVAE ACCORDING TO FEEDING HABITS

The structure of mouthparts, the method of feeding, and the habitat of the larvae are all inter-related (Mitchell 1906, Wesenberg-Lund 1921, Montchadsky 1937 and 1945, Hennig 1948, and Surtees 1959). On the basis of these factors culicine larvae have been classified into three types of feeders :

filter feeders, browsers, and predators

(Montchadsky 1936, Bates 1949, Surtees 1959). An ecological classification of mosquitoes was proposed by Shannon (1931), and a similar one by Marshall (1938) which was followed by Edwards et al. (1939), and Seguy (1950). This gives four groups of mosquitoes in Britain (Edwards et al. 1939): (a) Domestic species (hibernating in buildings). (b) Salt-marsh species (breeding on or near coasts). (c) Arboreal species (breeding in tree-holes). (d) Rural species (non-domestic, breeding in ground-waters usually away from coasts).

Students of mosquitoes have found that the environment plays an important role in determining what species can be successful in a particular area, Hopkins (1942), Haddow (1946), Twinn et al. (1948), Hocking et al. (1950), Goma (1960), and many others.

The classification of Surtees (1959) has been found convenient to follow in this work, and the criteria for classifying the mosquito larvae into filter feeders, browsers, and predators are summarized below.

1. 3. 1. Filter Feeders

The filter feeders have been defined as those species which strain out food particles from the surrounding medium, such particles being sufficiently small to pass directly into the digestive tract without undergoing any further breakdown. The salient morphological characters that distinguish filter feeders are as follows: long, fine, unserrated mouth brushes, large maxillae bearing many fine setae, small weakly chitinized mandibles, a weakly chitinized submentum possessing a large number of very small teeth, and associated with these features, large sub-apical tufts of setae on the antennae. These features of the labral brushes have been recognized by Wesenberg-Lund in several Danish species of mosquitoes:

Aedes cinereus, A. diantaeus, Culiseta morsitans, and in several species of Culex. This author found that the lateral brushes are divided into two parts, a horizontal and a vertical brush, which are separated from each other by a curve. When in action, the large horizontal rami of the lateral brushes are regularly thrust out and in, and are expanded and folded together. In the part held horizontally the hairs are pressed together and act against the water as a compact mass; in the part held vertically (the inner part) the hairs are spread out from each other during the stroke outwards, but undulating motions from without inwards may be observed during the strokes. By means of these undulating motions particles caught by the outer rami are carried downwards to the mandibles and then seized by them.

Nuttall and Shipley (1901) have described the function of the labral brushes of another filter feeder, an unnamed Anopheles species. According to these authors, all the hairs of the lateral brushes move together and both brushes move simultaneously as a rule. The hairs are arranged in a cupped fan-like shape, similar to a very strong, overhanging, arched moustache. The two brushes can move independently, and at times one is seen bent under while the other remains erect. The maxillae and the submentum form a chamber at the posterior end of which is the mouth opening. When the larva feeds the brushes are suddenly bent back into this space, the mandibles and the maxillae moving forwards to meet them and at the same time opening out, they are then suddenly released and fly back to their original position. This movement of sudden bending and swift relaxation is repeated with great rapidity, often some 180 times a minute, producing a current sweeping in convergent curves towards

the pre-oral chamber. The water filters out on each side, but any particle of food is retained by the complex of fine hairs which are borne by the mouth appendages. Furthermore, Nuttall and Shipley observed that from time to time the mandibles move close to the labral brushes and the stiff curved hairs of their upper edges are run through the brushes like fingers through the beard, and thus the curved mandibular hairs help to arrange the hairs of the brushes and keep them in their order. They may also assist in removing any particles of food that may be entangled in the brush. That this is of importance is shown by the fact that at intervals, generally at the end of a certain number of contractions the brushes disappear far into the mouth and are then slowly withdrawn, passing through the fine carding bristles on the inner faces and anterior edges of the maxillae. In this way any particle of food which may have become entangled on the brushes is carefully separated and remains on the mouth side of the maxillae. The brushes are frequently "swallowed" again and again and withdrawn in little jerks, so that the fine tooth-like hairs which act as a carding instrument have every opportunity to comb out any particles entangled in them.

From the position of the larva when feeding, the head with its brushes lies close below the surface film, the currents seem to be in a plane just below the surface film and to affect the organisms and organic debris which, being lighter than water, float up from the bottom of the pond or puddle and lie under the surface film. "In fact the larva sweeps the lower surface of the surface film of the water, just as a ceiling might be brushed to remove the flies and spiders which may have settled there." (Nuttall and Shipley 1901).

Feeding action similar to that observed by Nuttall and Shipley was also observed by Bekker (1938) in Anopheles maculipennis , and by Renn (1941) in A. quadrimaculatus and A. crucians. The characteristic anopheline feeding method where the floating particles approach the mouth along straight lines is referred to as the "interfacial " feeding pattern by Renn (1941). However, sometimes the anopheline larvae employ a feeding method which is common to the larvae of other genera of mosquitoes, and this Renn calls "eddy " feeding.

1. 3. 2. Browsers

The activity of the mouthparts of browsing larvae has been described by Mitchell (1906), Howard, Dyar, and Knab (1912), Wesenberg-Lund (1921), Surtees (1959), and Christophers (1960). Browsing by culicine larvae, according to Surtees, may be defined as the process of abrasion of solid material, the particles of which require further manipulation by the mouthparts before entering the digestive tract. The above mentioned authors agree that the browsing larvae are usually bottom feeders.

The labral brushes as well as the maxillary and mandibular bristles are shorter and stiffer than in the filter feeders, for as Mitchell (1906) says, in brushing over the debris at the bottom very long, slender hairs would be a disadvantage. When viewed from above , the labral brushes in action convey the impression of a compact brush with most hairs arranged in a semi-elliptical row, inserted nearest to the edges of the brush (Wesenberg-Lund).

The structure of the labral brush hairs varies. The more median bristles are curved, flattened, and bear several teeth on the inner

side (ten to twenty) (Wesenberg-Lund 1921, Salem 1931). These hairs are used as a comb apparatus to move the larva and bring food in the current. Often the larvae are found in ponds with small volumes of water. They go down to the bottom where they brush and comb off the sedimented particles from the decaying leaves, using this material as food. This applies mostly to the larvae of Ochlerotatus (Wesenberg-Lund). Mitchell (1906) and other authors have also observed browsing larvae brushing over the sides of containers or floating or half submerged objects, grasses, Spirogyra, etc.

Mandibles are used to manipulate any large particles that come into the feeding stream, and the submentum is used as a secondary grasping organ. The swimming position is usually at an angle of about 45° to the substratum.

Intergradations occur between typical filter feeders and browsers (Wesenberg-Lund 1921 , Surtees 1959). For example, Surtees observed some indications of browsing characteristics in a few filter feeders, mainly in the development of shorter labral brushes and coarser maxillary setae, together with the loss of the sub-apical antennal setae. In the genus Culex, two species which are usually found in larval environments rich in decaying vegetable matter are C. nebulosus Theobald and C. cinereus Theobald, both browsing species. These retain some of the filter-feeding characters in combination with others which are typically part of the browsing facies. The mouth brushes are short but not serrated and the sub-apical antennal tufts are lost, while the mandibles possess a row of strong setae. The maxillae are still rela-

tively large but the palpus is small. Surtees cites similar examples from the genus Aedes.

1.3.3. Predators

Predators are those larvae that attack and feed on the larvae of other species or sometimes younger instars of their own species (Surtees 1959). The predatory culicine larvae are represented by the genera Toxorhynchites and Eretmapodites, the Culex and Aedes sub-genera Mucidus and Lutzia, and the Sabethes, and Psorophora groups of mosquitoes. (Giles 1902, Theobald 1903, Mitchell 1906, Bates 1949, Surtees 1959). In these predatory larvae the role of the maxillae has been further suppressed and the mandibles have become the mouthparts of major importance. The labral brushes are usually strongly chitinised and scissor-like in form but in Culex tigripes Grandpre they are heavily serrated and the mandibles are the main prehensile organs. The typical predatory facies can be seen in Toxorhynchites brevipalpis Theobald. The number of mouth brushes has been reduced concurrently with their increase in strength, and they are gathered into one series only, features which facilitate their prehensile and raptorial function. Breland (1949) observed no raptorial function in the larvae of Megarhinus septentrionalis D. & K. The mandibles are very large with strongly chitinised claws and take up most of the oral region of the head capsule. Associated with the strong claws are large, stiff spines which also aid in grasping the prey. This is also true of the Chaoborus and Mochlonyx larvae (Schremmer 1950, Peterson 1951, Cook 1956, and others). The development and arrangement of these setae differ from species to species.

The submentum in all predatory species is well developed, the teeth being large and generally pointed. The increase in the strength of the submentum is associated with a reduction in the number of teeth as with the mouth brushes. The maxillae in all these species are reduced in size but have strong setae. The palpi are typically small and strongly built (Surtees, 1959).

1.4. EVOLUTION

The adaptation of structural characters to the environment of the larvae and adults has been discussed by various authors, one of the early ones being Mitchell (1906). Montchadsky (1937) discusses at length the evolution of the larvae and its relation to the evolution of adult mosquitoes within the family Culicidae. Larval as well as adult characters are used to divide the family Culicidae into the subfamilies Chaoborinae and Culicinae, and the subfamily Culicinae into tribes Anophelini, Megarhinini and Culicini.

The type of feeding represents a factor which ties into one the processes of evolution of larvae and the adult mosquitoes. The types of feeding of each of their feeding phases of development are mutually conditioned. Their changes in one phase bring about compensatory changes in another phase. Representatives of the primitive family Dixidae have vegetarian larvae leading an amphibiotic life, and non-bloodsucking adults which feed on plant juices. In the subfamily Chaoborinae the adults remain plant feeding while the larvae become predators, giving two lines of adaptation to predation - the surface film - e. g. Eucorethra, and the pelagic-e. g. Chaoborus.

Most representatives of the subfamily Culicinae on the other hand, have plant-feeding larvae with various degrees of adaptation to

existence in one medium, and have adults adapted to sucking the blood of vertebrates, (Montchadsky 1937, Hennig 1950). However, there are groups within this subfamily which have reversed their type of feeding. For example, in the genera Megarhinus and Lutzia and others the larvae lead a predatory life, but have in their structure a series of characteristics which indicate a previous adaptation to a vegetarian type of feeding. The adults of these mosquitoes either feed on plant juices, but carry traces of previous ability to suck blood, or appear to be optional blood feeders (Montchadsky 1937).

Hence the initial stages of evolution of the family are connected in a way whereby either there is a change in the type of feeding of the adults (e.g. transition to blood feeding in the subfamily Culicinae, or in the larvae - the transition to predation in the subfamily Chaoborinae). According to Montchadsky (1937) these changes were apparently provoked by some changes in the conditions of the ripening of the sexual glands, connected with the rise of necessity for the higher quality albumin. Cases of secondary changes in the type of feeding in some groups of the subfamily Culicinae apparently were provoked by peculiarities of the biology of larvae which live under conditions of small enclosed accumulations of water with an unstable food condition.

According to Montchadsky (1937) and others, the principal direction of evolution of the larval mosquitoes appears to be a gradual adaptation to exist deeper within a water medium in the conditions of adaptation to some type of feeding. This is found

to be related to the feeding habits of the adult mosquitoes. These authors maintain that if adequate food containing high quality protein is eaten by the predatory larvae, it is not required by the adults of the same species, hence the adults are vegetarians. On the other hand, the non-predatory mosquito larvae do not obtain adequate high quality protein, therefore the adults of these species must have it from the blood of vertebrates. This explanation of the evolution of feeding habits of mosquito larvae and adults seems reasonable, although it may not be the complete explanation of the phenomenon.

2.0 MORPHOLOGY OF THE HEAD AND MOUTHPARTS OF MOSQUITO LARVAE

2.1. INTRODUCTION

Since the structure of animals is intimately related with function, a knowledge of the structure of mosquito larval mouthparts was necessary if their function was to be studied and understood. It was difficult to decide which nomenclature to use for the different mouthparts. Since most disagreement occurs in the interpretation of the parts of the maxilla and the labium, it was essential to pursue the study of homologies so that a reasonably accurate interpretation of the larval mouthparts could be reached. It was necessary to compare the mouthparts of mosquito larvae with the larval mouthparts of other Nematocera, Mecoptera, and with the larval mouthparts of other Panorpid groups. Since a limited number of representatives of other Nematoceros larvae and no specimens of Panorpa or other Mecopterans were available, I was largely dependent on the published descriptions of them.

2.2. PROCEDURES

Two species of mosquitoes, Aedes aegypti (L.) and Guliseta inornata (Williston) were reared in the laboratory, so that fresh specimens of these species were almost always available. Rearing methods of Tremblay (1955) and McLintock (1952) were followed.

Living specimens were also collected in the field and observed, preserved, and dissected in the laboratory. The larvae were preserved in either 70% ethanol or in 70% ethanol plus 5% glycerine. For imbedding and for some of the dissections, larvae were fixed in one of three fixatives: Dietrich's solution, Bouin's and a special fixative of Griffiths & Carter (1958). In sectioning the larval heads the best results were obtained with the last mentioned fixative. The following histological references were consulted: Carleton & Drury (1957), Pantin (1960). Sectioned material was found to be more difficult to interpret than dissected material, and since larvae were available in abundance, dissected larval heads were mostly studied. The dissections were done in glycerine. Hoyer's mounting medium (Beirne 1955) and neutral Canada Balsam were used for mounting the mouthparts. Eosin - water solution was used for staining dissected muscles, and Mallory's trichrome method (Pantin 1960 and modified by Petersen 1960) was used for staining larval head cuticle.

The morphology of the heads of the larvae of Aedes fitchii (F. & Y.) and Culiseta inornata (Williston) was studied in detail, and other species, listed in Table 2, of mosquito larvae were compared with these species. In this section the larval head and mouthparts of Aedes fitchii (F. & Y.) are described and differences found in the other species that were studied are pointed out. Larvae of a Chironomus species, Mochlonyx velutinus (Ruthe), and Chaoborus americanus (Johannsen) were also examined.

Figures were obtained in three ways: from specimens placed under the binocular microscope and drawn with the use of a squared grid in the eyepiece of the microscope; from photographs and from free-hand sketches.

2. 3. DESCRIPTIONS OF THE HEAD AND MOUTHPARTS OF MOSQUITO LARVAE

2.3.1. The Head Capsule

The largest sclerite in the head capsule of a mosquito larva is the frontoclypeus, and it extends over most of the head surface dorsally. Laterally the head capsule consists of the genae, and postero-laterally of the postgenae which unite and extend ventrally to complete the head capsule (Hennig 1948, Snodgrass 1959, and others) (Figs. 1, 2, 3). The median ventral part of the united postgenae, posterior to the mouth, is given different names by various authors. I consider it as the subgena. It is bounded by two lines of cuticular thickening ridges (Figs. 2, 9, r), which are known variously as the submental-postgenal sutures (Shalaby 1956 and 1957 a, b, c, d, respectively in A. quadrimaculatus, A. aegypti, C. quinquefasciatus, Psorophora ciliata and C. molestus); hypostomal sutures (Menees 1958, in Anopheles quadrimaculatus, Christophers 1960, in Aedes aegypti); and thickening ridges (Snodgrass 1959). On the nomenclature of these ridges I agree with Snodgrass mainly because I also agree with his interpretation of the homologies of the ventral head sclerites. In homologising these head sclerites of the mosquito larva Snodgrass digresses to discuss the ventral head sclerites of other insects, especially insects

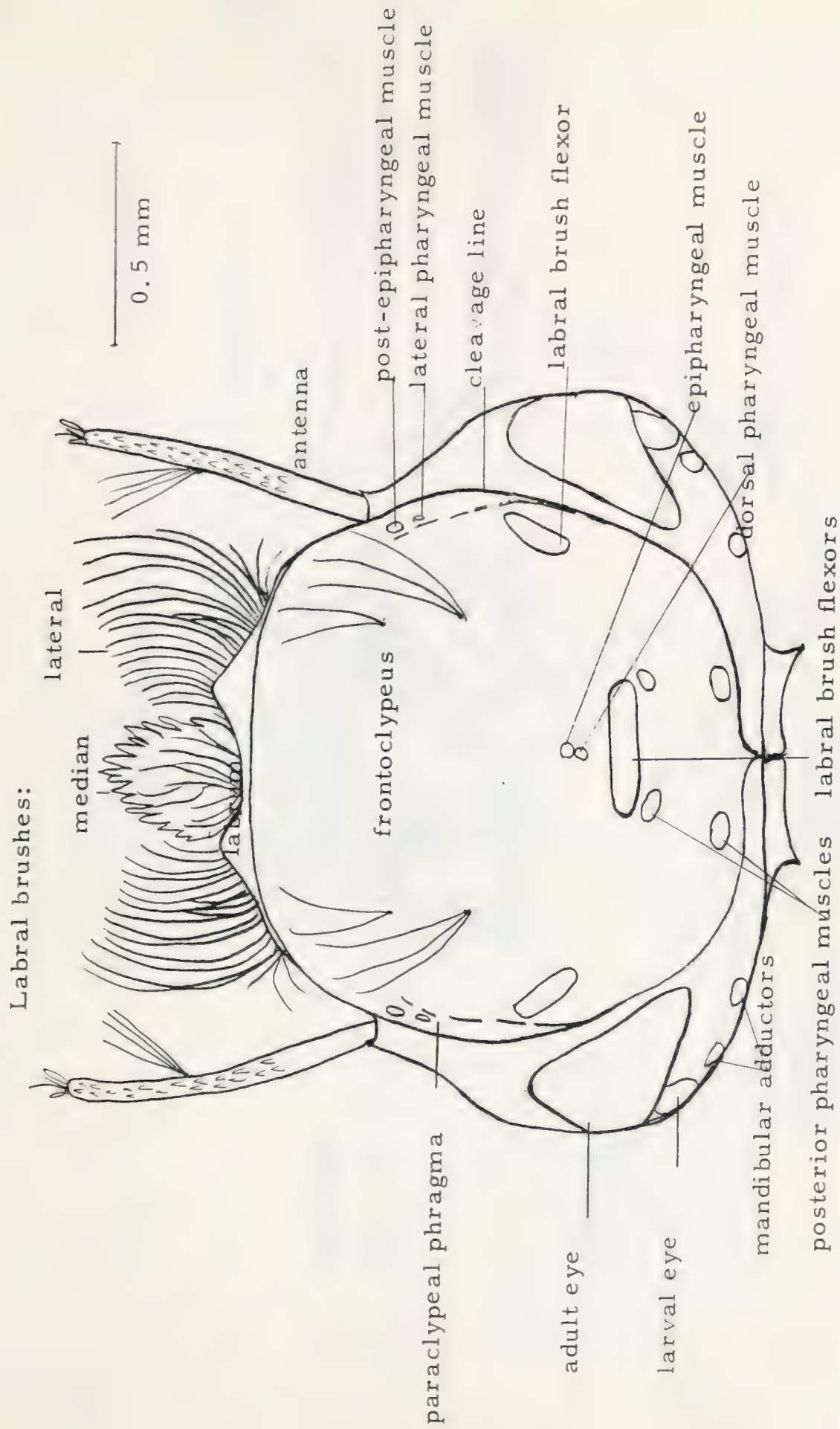


Fig. 1. Dorsal view of the head of Aedes fitchii (F. & Y.) larva, showing muscle origins and extended labral brushes.

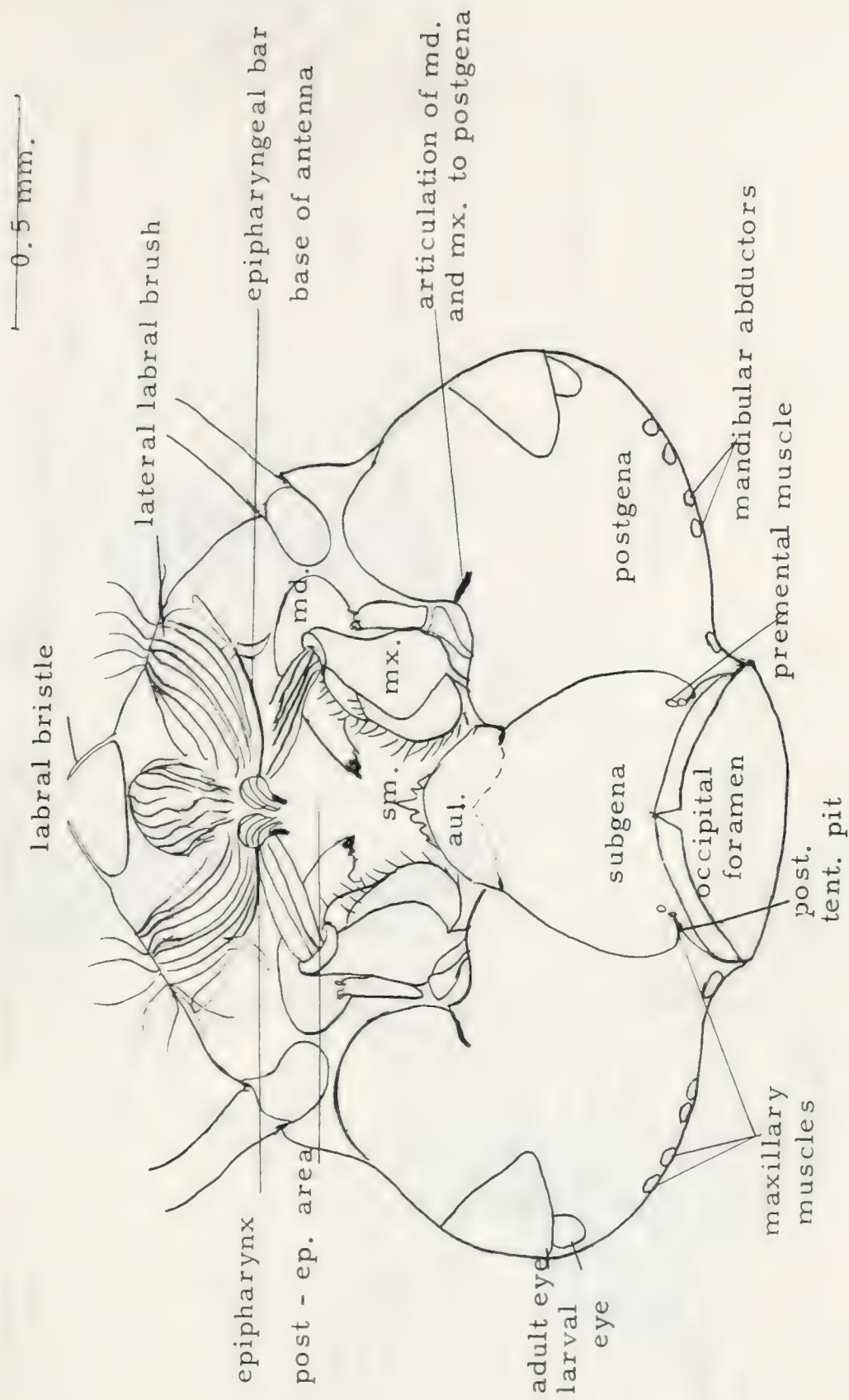


Fig 2. Ventral view of the head of *Aedes fitchii* (F. & Y.) larva, showing some muscle origins and retracted labral brushes. Abbreviations : aul.- aulaeum; md.- mandible; mx.- maxilla; post-ep.- post epipharyngeal; post. tent.- posterior tentorial; sm.- submentum.

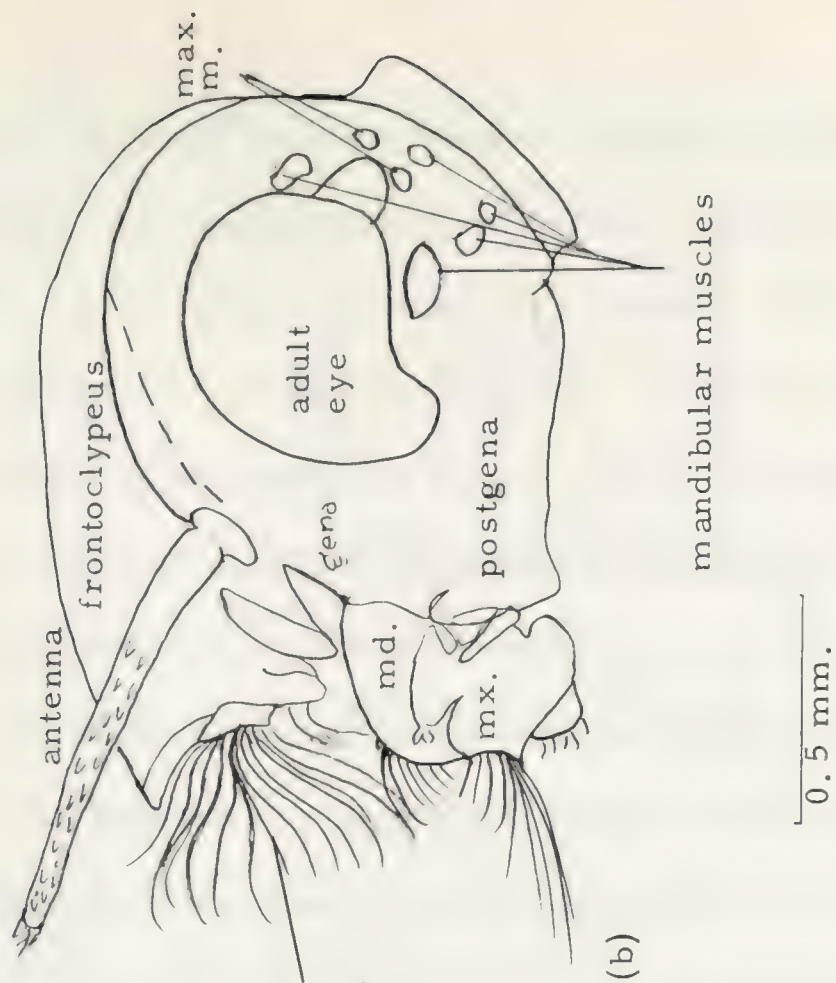
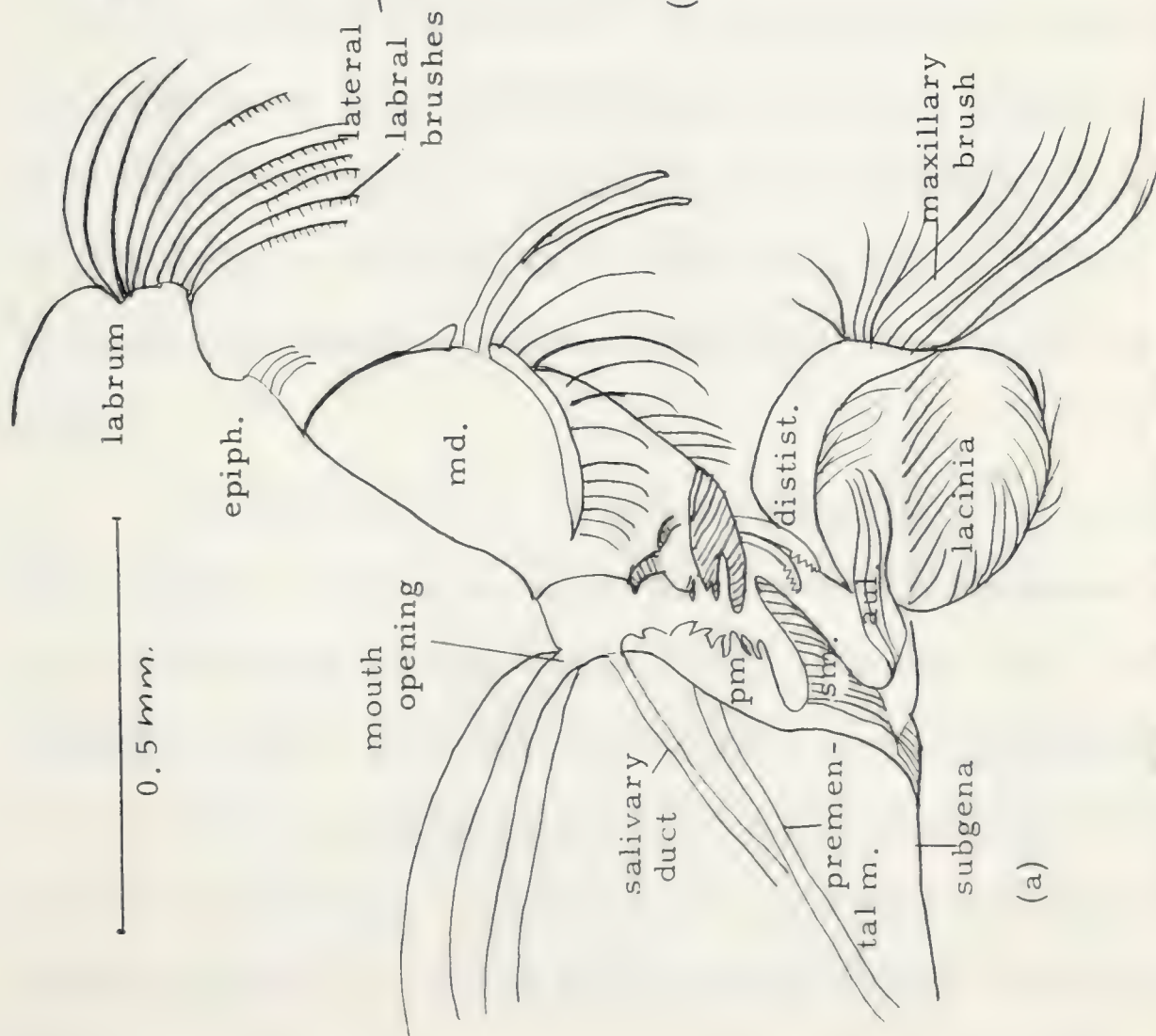


Fig. 3. (a) The mouthparts of *Aedes fitchii* (F. & Y.) larva, as seen from the sagittal plane.
 (b) Lateral view of the left side of the head of *A. fitchii* larva, showing mandibular and maxillary muscle origins.

Abbreviations: distist.- dististipes; epiph.- epipharynx; m.- muscle; pm.- prementum. Others are same as in Fig. 2.

in which a trend toward a ventral elongation of the postgenae is evident. As examples he cites certain beetles in which the entire labium with a gular addition to the submentum is enclosed between the postgenae. He states, however, that this condition is not represented in the mosquito larvae. More commonly, the postgenae come together medially and displace the labium, and a primary stage of this condition occurs in the head of a caterpillar or an adult honey bee where the lobes of the hypostomal margins of the postgenae are intruded between the occipital foramen and the base of the labrum. In other instances the postgenae unite to form a bridge between the occipital foramen and the labium. In some beetles an elongation of the bridge can be seen while the labium is still fully exposed. A final example in this series of changes is represented by the larvae of Chironomidae where the labium has become greatly reduced and is hidden from below by a median hypostomal lobe of the united postgenae.

A similar process of closure and elongation of the postgenae and reduction of the labium occurs in nematoceros larvae as is discussed by Anthon (1943), Hennig (1948, 1950, and 1952), and Snodgrass (1959). In the primitive rhyphid larva of Olbiogaster (Anthon 1943), the small postgenal lobes approximate behind the submentum of the labium. In tipulid larvae, described by Vimmer (1906) and other authors, as well as in other nematoceros larvae the genae

are completely united ventrally and the labium is located above the subgenal lobe. In the mosquito larva, to distinguish the ventral area between the thickening ridges of the genae Snodgrass names this area the subgena, and the areas laterad of the ridges the postgenae. I follow the same nomenclature of these sclerites.

Cook (1944, 1949), following Ferris's (1947) and Henry's (1947) theories of the segmentation of arthropod head, considers the postgenae and the subgena as parts of the maxillary segment. Shalaby (1957) considers the apical part of the subgena as the mentum and the remainder as the submentum. As evidence for this idea Shalaby refers to Wheeler's (1893) embryological work in which the latter observed that the rudiments of the second pair of maxillae on the sides of the embryonic body give rise to the labium in the embryos of the locust Xiphidium ensiferum Scudder, in Gryllus luctuosus, and Stagmomantis carolina. Shalaby believes that the median suture present on the ventral sclerite of the head of Culex molestus larva is due to incomplete fusion of the embryonic rudiments of the second maxillae. That the embryonic second maxillae give rise to the labium has been shown by Butt (1957) in Oncopeltus, and by other authors working on other insects. But Menees (1958 a), studying the embryonic development of Anopheles quadrimaculatus, observed that the median suture on the ventral head sclerite in this species is the result of incomplete fusion of the postgenae.

Christophers (1960) also believes that the sclerite which Snodgrass and I consider to be the subgena is the labial area, and he interprets the subgenal areas posterior to the maxillae as fused bases of the maxillae (cardo and stipes). Christophers thus believes that in the larval as in the adult stages of mosquitoes the bases of the maxillae extend to the occipital foramen, forming the hypostomal area. However, the sclerite which Christophers considers as the base of the maxilla serves as origin of pharyngeal, mandibular, and maxillary muscles which in other insects usually originate on the tentorium or the cranial wall (Snodgrass 1935). In the adult mosquito, Aedes vexans, as described by Peterson Hoyt (1952), the maxillary muscles originate on the tentorium. On the other hand, none of the postgenal muscles of the mosquito larva originate on the tentorium. If the larval postgena is to be considered as the fused maxillary cardo and stipes, then the origins of the various muscles upon it, mentioned above, are difficult to explain.

Most head sutures which are characteristic of the primitive insect head are absent from the heads of mosquito larvae. Two cleavage lines extend anteriorly from a short posterior occipital stem (Fig 1). According to Snodgrass (1959), cleavage lines are lines of weakness in the cuticle where a split takes place at ecdysis to allow the emergence of the next instar. These cleavage lines may be homologous with the frontal suture and the epicranial suture of other insects. However, Snodgrass (1947 , 1958) and DuPorte (1953) state that the frontal arms of this suture follow diverse paths

in different insects, that they can have no morphological significance, and therefore do not define any specific part of the head. For this reason, in this work head sclerites and mouthparts have been named in reference to muscle origins.

The large dorsal sclerite of the mosquito larval head has been variously named as the frons, the clypeus and the fronto-clypeus (Table 1). Approximately in the center of this sclerite arise the labral and epipharyngeal muscles which usually originate on the clypeus, and somewhat posteriorly to these are the origins of the pharyngeal muscles which generally occur on the frons.

In the head of Aedes fitchii (F.&Y.) larva, as well as in the larval heads of all the other mosquitoes examined, there is no demarcation between the areas where the different muscles originate, therefore, it seems reasonable to call this sclerite the frontoclypeus.

The tentorium in the mosquito larva is represented by anterior and posterior arms. The anterior arms originate on the head capsule lateral to the antennae, in the same area where the hypopharyngeal bars arise. The long, slender anterior tentorial arms connect to the short posterior arms on the postero-ventral part of the head. There is no tentorial bridge.

On each side of the head a hypopharyngeal bar connects the hypopharynx to the side of the cranium (Fig. 9).

2.3.2 The Labrum

The labrum of the larva of Aedes fitchii (F.&Y.) consists of a narrow transverse sclerite dorsally (Fig. 1). Ventrally it is

composed of a membranous area to which three brushes are attached; one median and two lateral movable brushes. The median brush is connected to each lateral labral brush and to the dorsal part of the labral sclerite by a membrane which Christophers (1960) calls the tessellated membrane (Fig 5, t.m.) As in A. aegypti, described by Shalaby (1957a), so in A. fitchii two types of hairs are found on the median brush; long thin branched hairs posteriorly, and short stout hairs with serrated distal ends anteriorly. Both types are shorter on the lateral sides of the brush than medially.

The lateral labral brushes are composed of four types of hairs which differ in length, thickness, curvature, and location. The hairs of the first type are simple, relatively short, thin, soft, without definite curvature, and are located on the edges of the postero-lateral and dorsal sides of each brush and on the ventral median sides, overhanging the pharynx (Figs. 4, 17, 18.). These hairs, which are attached to the tessellated membrane, do not take part in creating a feeding current, but they can be moved by the flowing water of the current. Hairs of the second type are long, simple, thin, slightly curved at their bases and at their distal ends, and are located on the lateral posterior two thirds of the brush (Fig. 4.). These hairs take an active part in creating currents. The shortest, thickest hairs of the brush are type 4 hairs, found in the anterior median region of the brush. The bases and apices of these hairs and also of type 3 hairs lateral to them are provided with serrations (17 - 20 per hair).



Fig. 4. Ventral view of the labrum of the larva of *Aedes fitchii* with the lateral labral brushes extended.



Fig. 5. Ventral view of the labral area of the larva of Culex territans Walker, with the bases of the brushes extended to show the cross bars to which the hairs are attached.

The serrations on type 3 hairs are smaller and slightly closer to each other than those on type 4 hairs. Four types of hairs were found in all the browsing species of Aedes and Culiseta except in A. cinereus Meigen and A. canadensis (Theo.) which have all short, simple hairs on their lateral brushes. When the labral brushes are stained with Mallory's triple stain the bases of all the hairs stain red. Next above the bases a narrow layer of blue appears across the hairs and above this layer hairs of type one and two stain red to their tips. Hairs of type three and four stain partly red above the blue portion, but both types stain blue apically in their serrated regions. A large proportion of the most median type four hairs stains completely blue above the red bases. In A. fitchii (F. & Y.) and the other Aedes larvae as well as in the Culiseta browsing larvae that were examined the apices of hairs of type one and two are tapered. Also tapered are the apical ends of all the hairs of the labral brushes of the filter feeding Culiseta and Culex larvae (Culiseta morsitans (Theo.) and Culex territans Walker). There is no subdivision into serrated and unserrated hairs in the brushes of the filter feeding larvae; all the hairs are simple. They all have red staining bases, blue-staining portions above the bases, and red-staining middle and apical portions. In the filter feeding larvae a large group of hairs, originating medially on each lateral labral brush, overhangs ventrally, partly covering the epipharynx. A smaller number of simple hairs extends in this position in the browsing larvae (Fig. 17). In all the larvae that were examined these hairs are red-staining. In the larva of Chaoborus americanus (Johannsen) the labral brushes consist of a few hard, short, brown bristles on the small labral

sclerite. In the larva of a Chironomus species a few labral bristles are red-staining and the remainder are blue-staining.

Manton (1958) commented on the staining reaction of cuticle with Mallory's triple stain and concluded that sclerotized non-staining exocuticle is unstretchable when thick, and red-staining cuticle is less fully sclerotized, less rigid, and more elastic than the non-staining cuticle. The pale blue-staining cuticle is flexible but not elastic. Thus the staining reaction of the labral brushes of the filter feeding and browsing larvae indicates that their hair bases are elastic and the portions above the bases are flexible. Flexibility of these hairs was seen when living larvae were observed in feeding activities. Also the differential flexibility was noticed when the hairs were touched with a needle.

In the mosquito larvae examined all the hairs of the lateral brushes (except for type one of which very few are present) are attached to sclerotized rods which extend transversely across the basal area of the brush (Figs. 5 & 6). Christopher's term for these rods, "cross bars," is used in this work. On each lateral labral brush of A. fitchii larvae between forty-five and fifty of these bars are present, and each bears approximately twenty hairs. Therefore each lateral brush contains nearly a thousand hairs. A similar number of hairs is present in the lateral brushes of C. inornata larvae.

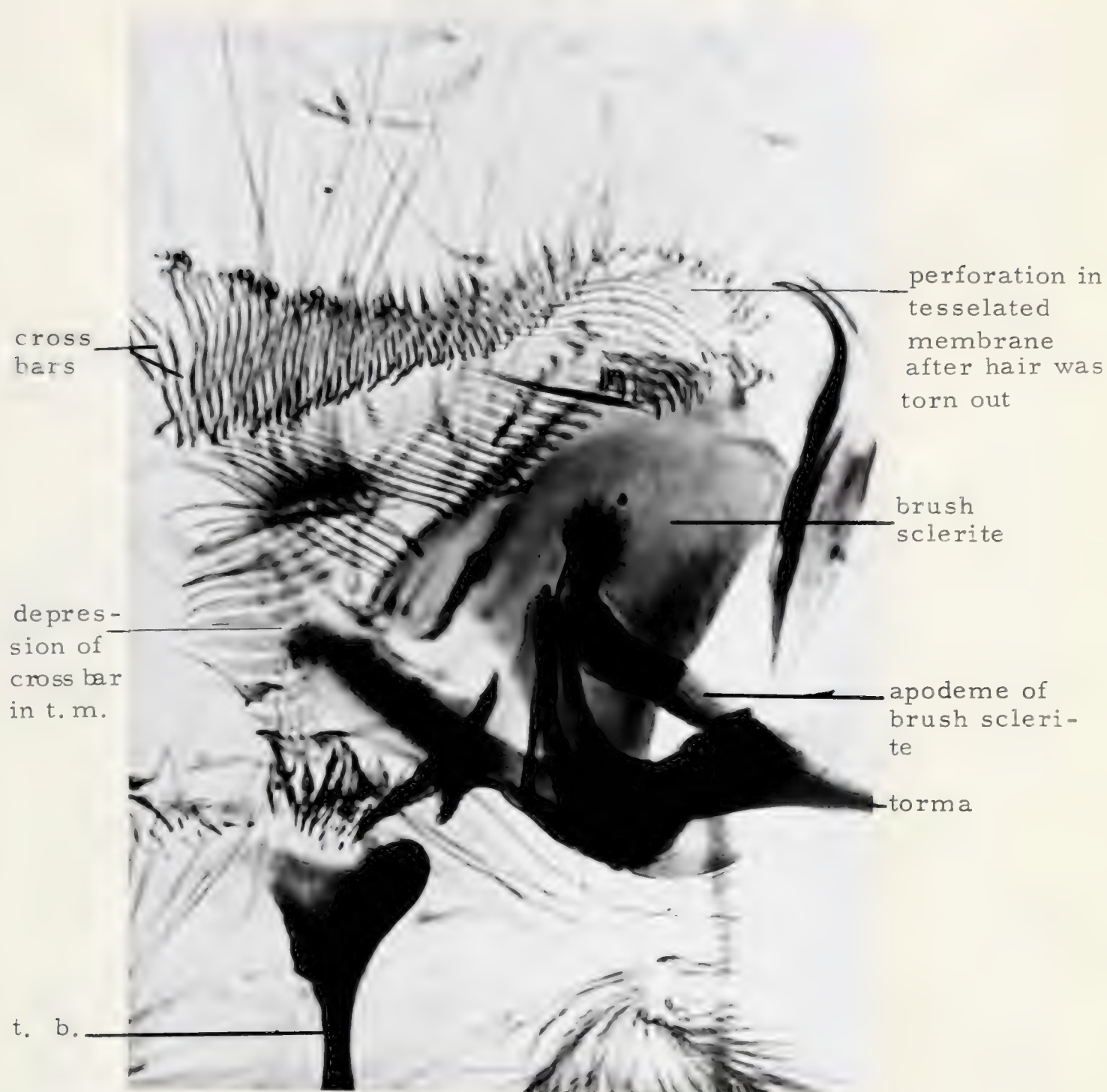
The cross bars are cuticular thickenings of the tessellated membrane (Fig. 6 (c) i) with their distal parts ending freely in this membrane, next to the dorsal sclerite of the labrum (Fig. 6 (c) iv & v). When the cross bars are pulled away from the tessellated membrane and the hairs,

depressions where the hairs were attached can be seen on them (Fig. 6(b)).

The proximal end of each cross bar is curved into a hook (Fig. 6 (b)); it terminates in the brush sclerite which is roughly triangular and is attached to the median part of the torma by an apodeme (Fig. 6 (a)).

Muscles that move this sclerite insert on the posterior tormal apodeme which is attached to the posterior end of the torma (Fig. 9). Contraction of the labral muscles exerts tension on the brush sclerite which in turn pulls the tessellated membrane and the cross bars by their hooks. This causes the hairs of the brush to move ventro-medially. The hairs spring back outwardly through the elasticity of the tessellated membrane. The inward and outward movement of the hairs is thus caused by the differential elasticity of the tessellated membrane and the cross bars. The bases of the hairs are connected with the cross bars and fork on either side of them (Fig. 6 (b) & (c)ii). The bifurcations are short (Fig. 6 (c) vi), and their ends terminate in the tessellated membrane below the cross bars (Fig. 6 (c) ii). The stretch of the tessellated membrane allows the part of the hair which is attached to the rigid cross bar to move more than the tips of the fork, so that the hair pivots about this attachment to the cross bar, and its tip swings ventro-medially. Relaxation of the labral muscles allows the hairs to return to their original positions through the elasticity of the tessellated membrane.

The angle through which a hair swings should increase with its distance from the brush sclerite since it is separated from this by a greater length of the elastic membrane. This would have the effect of bunching the hairs together in the median position and allowing them to fan out in the lateral position, which was repeatedly observed to happen. When the hairs are pulled off the membrane, their forked bases, the



(a)

0.50 mm.

Fig. 6. Details of labral hair attachments of the larvae of Culex territans (a) and Aedes fitchii (b). t. b. - transverse bar, t. m. - tessellated membrane.



(b)

0.50 mm.

Fig. 6. continued

Different types
of cuticle:



non-staining



stiff
stains red



flexible
stains blue

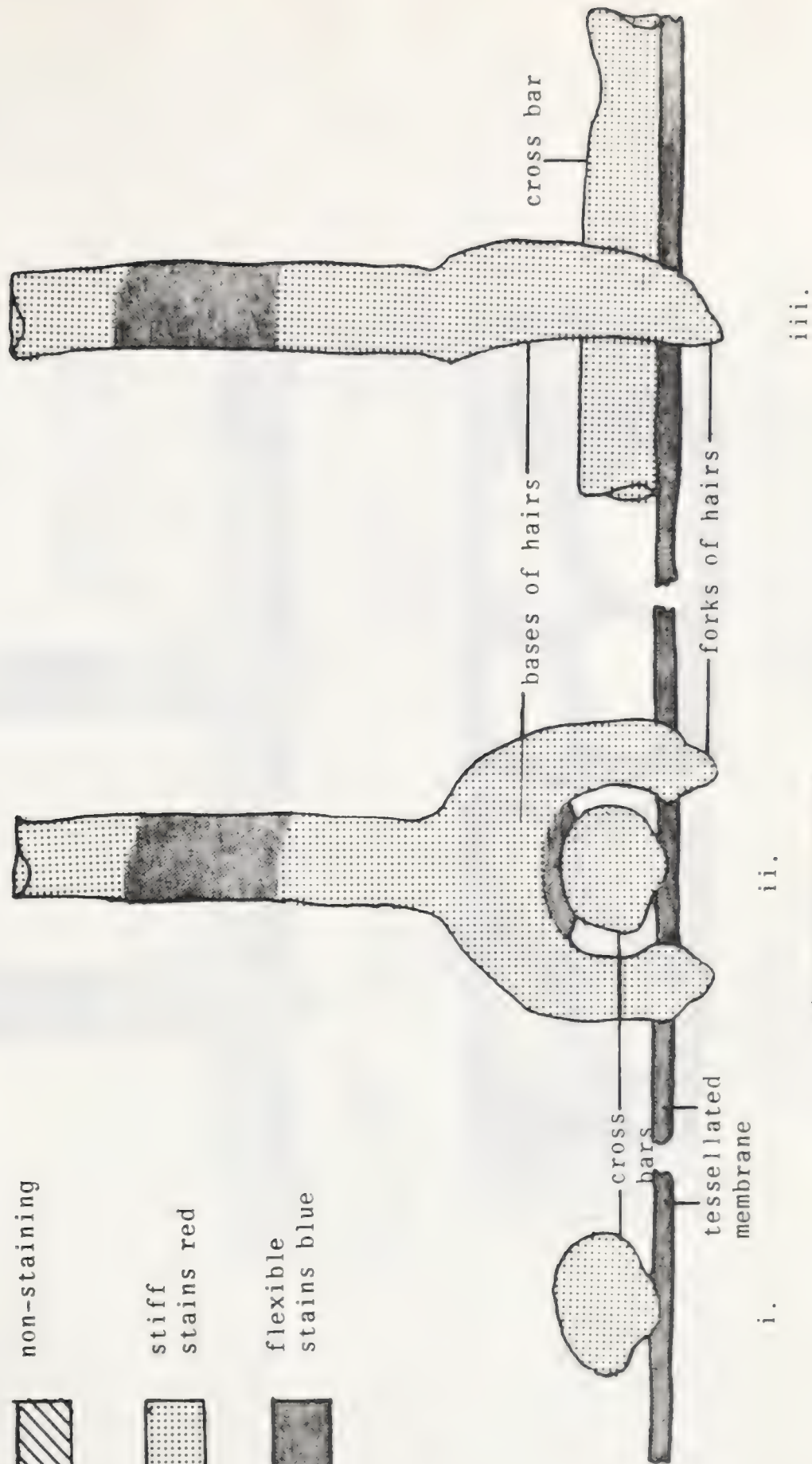


Fig. 6 (c). Diagrams of hair bases of the lateral labral brush of a mosquito larva. i. Traverse section of the tessellated membrane and its thickening, the cross bar. ii. Transverse section of a part of a hair and its attachment to the tessellated membrane and the cross bar. iii. Longitudinal section of a cross bar and hair base.

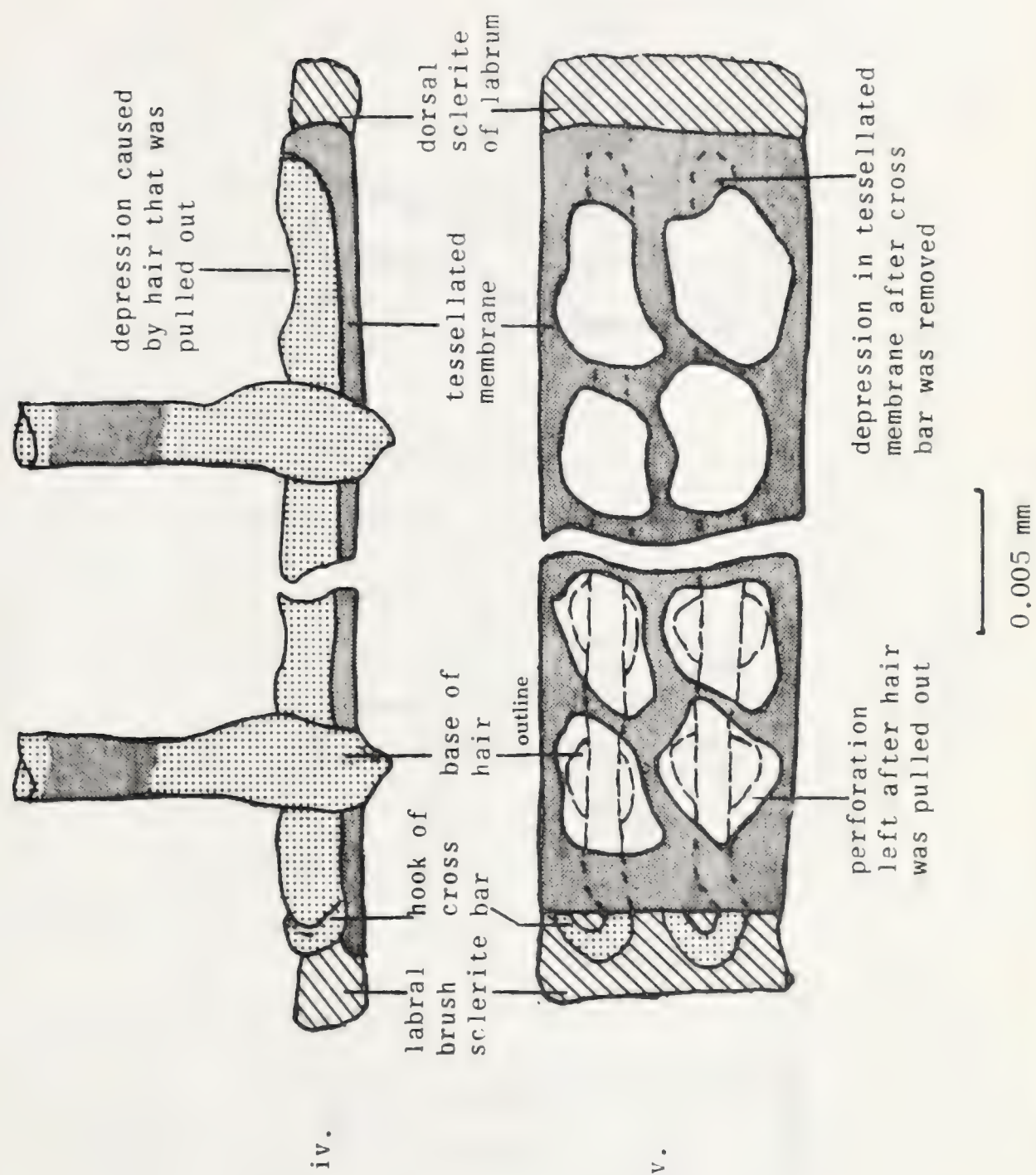


Fig. 6 (c). Diagrams of the hairs of the labral brush and the cross bars showing attachments to the tessellated membrane and to the labral sclerites. iv. Lateral view. v. Surface view.

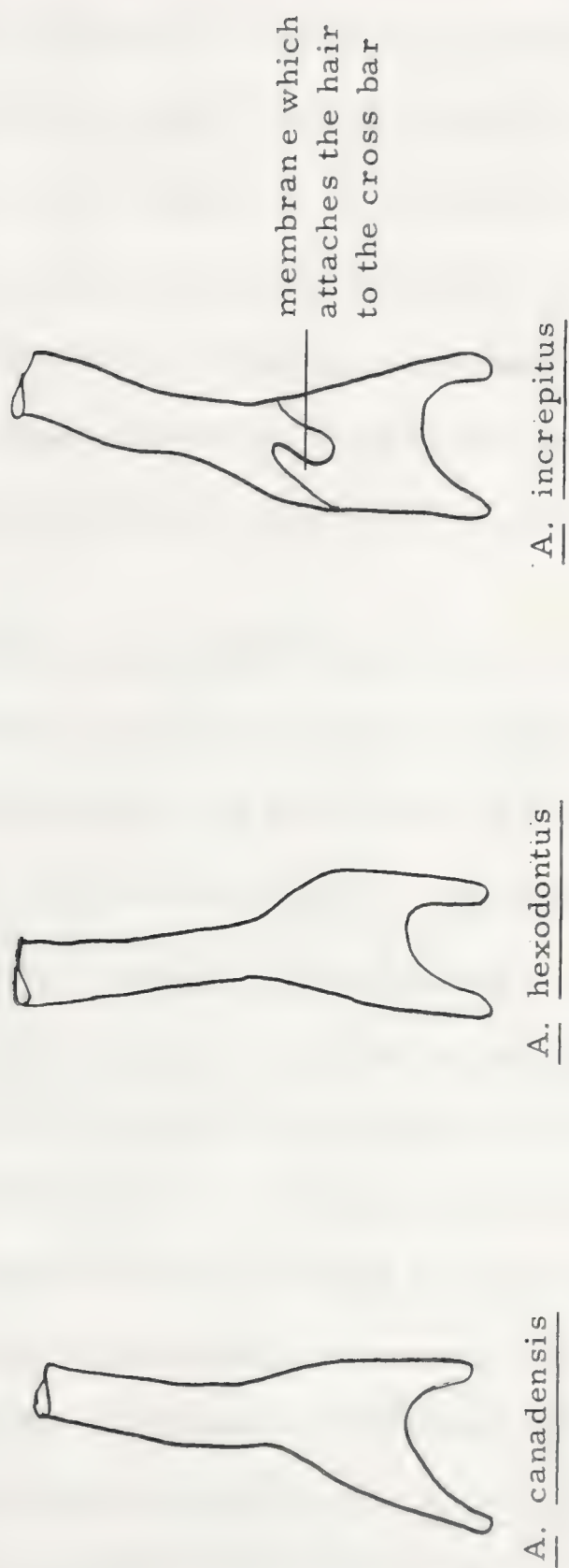


Fig. 6 (c) vi. Diagrams of labral hair bases of *Aedes* larvae. Anterior views are shown.

cross bars, and the membrane between these come with them. This leaves rounded holes in the membrane and confirms that the cross bars are more strongly attached to the hair bases than to the membrane. The cross bars leave depressions in the tessellated membrane (Fig. 6 (a) & (c)v). It was because of the pattern that the rounded perforations give to the membrane, that Christophers (1960) named it the tessellated membrane. However, in the specimens examined the shape of the holes was not always rhomboid or square. Pentagonal, hexagonal, oval, and roughly circular shapes were also seen in the same membrane. Sometimes the mounting medium and the cover slip cause considerable distortion of the structures.

When this complex is stained with Mallory's triple stain the following parts stain red indicating rigidity: the cross bars and the hair bases; while the tessellated membrane and small parts of the hairs above their bases stain blue, indicating elasticity. The edges of the holes may be outlined in red perhaps because of some change in the character of the material of the membrane resulting from its tearing.

The ends of the epipharyngeal bar are attached to the posterior parts of both tormae (Figs. 5 & 17). From the anterior end of the torma a narrow sclerite projects medially towards a similar projection from the other torma. These sclerites (Figs. 5, 6 (a), & 17, t.b.) are commonly known as transvers bars (Shalaby 1957 a) or palatal bars (Christophers 1960). The structure of these bars in A. fitchii is slightly different from that in A. aegypti as described by the above authors. In A. aegypti the bars are slender and from each one a small curved sclerite projects anteriorly. In A. fitchii the bars are

stout and curved medially, and are attached by thin sclerites to the tormae (Fig. 4, t. b.). The transverse bars in the Culex territans larva are wide basally, narrow medially, and are attached to the tormae by thin sclerites (Figs. 5, 6(a), t. b.). The transverse bars of this species of Culex are not curved medially as those of the Aedes species.

In the species examined only the posterior apices of the tormae stain blue; the remainder of these structures with their apodemes retain their brown color. Thus the tormae and their apodemes are rigid, highly sclerotized structures. The associated membranes stain light blue.

In the predatory Chaoborus americanus (Johannsen) larva the labrum is greatly reduced, no labral brushes are present, but a few short stiff bristles are found at the tip of the labral sclerite (Cook 1956). These bristles stain dark red.

2.3.3. The Epipharynx and the Preoral Cavity

The structure of the epipharynx in the species examined is very similar to that described by Shalaby (1957 a) and Christophers (1960) in A. aegypti. In A. fitchii (F. & Y.) and the other browsers the hairs are coarser than in Culiseta morsitans (Theo.) and Culex territans Walker. The spines and hairs stain dark red in A. fitchii which indicates medium hardness; they stain lighter red in C. morsitans (Theo.) and C. territans Walker, indicating less hardness. The epipharyngeal bar stains medium blue in all specimens. That this flexible structure can move anteriorly and posteriorly has been observed in living larvae of A. aegypti (L.) and Culex territans.

The post-epipharyngeal area consists of a membrane between the epipharynx and the pharynx. It is similar to that described by Cook in Theobaldia incidens (Thomson) (= Culiseta incidens), but a difference in the number of muscles inserting on this membrane was observed. In T. incidens two muscles are present in the area between the epipharynx and the pharynx, but in A. fitchii three muscle strands (Fig. 7) are present. Since these muscle strands have a common origin on the cranium, medially of the antenna (Fig. 1), I consider them as fascicles of one muscle.

2.3.4. The Mandibles

The mandibles of Aedes fitchii (F. & Y.) larvae consist of flattened, roughly quadrilateral lobes with their mesal ends produced into strongly sclerotized toothed processes and lower seta-bearing lobes. Essentially they are similar to the mandibles of most culicine larvae which have been described by other authors (Shalaby 1957, Snodgrass 1959, and others).

Large comb-like fringes (Fig. 8 (b), Md. c.) of long mesally directed setae are borne on their dorsal margins. These setal fringes are called mandibular combs by Shalaby (1957) in his description of A. aegypti (L.). In each comb of A. fitchii (F. & Y.) eleven curved, sharply pointed and pigmented stout setae are present; in Culiseta inornata (Will.) nine such setae are present; and in A. aegypti (Shalaby 1957a) fifteen setae are present in the 4th ~~instar~~ larval mandible. Another series of setae (Fig. 8 (b) Md. B) extends meso-dorsally from the medial side of the mandible, medially of the lateral bristles (MdBr), and this series Shalaby names the mandibular brush. In C. inornata it



Fig. 7. The epipharynx and the post-epipharyngeal area of *Aedes fitchii* larva with its muscles.

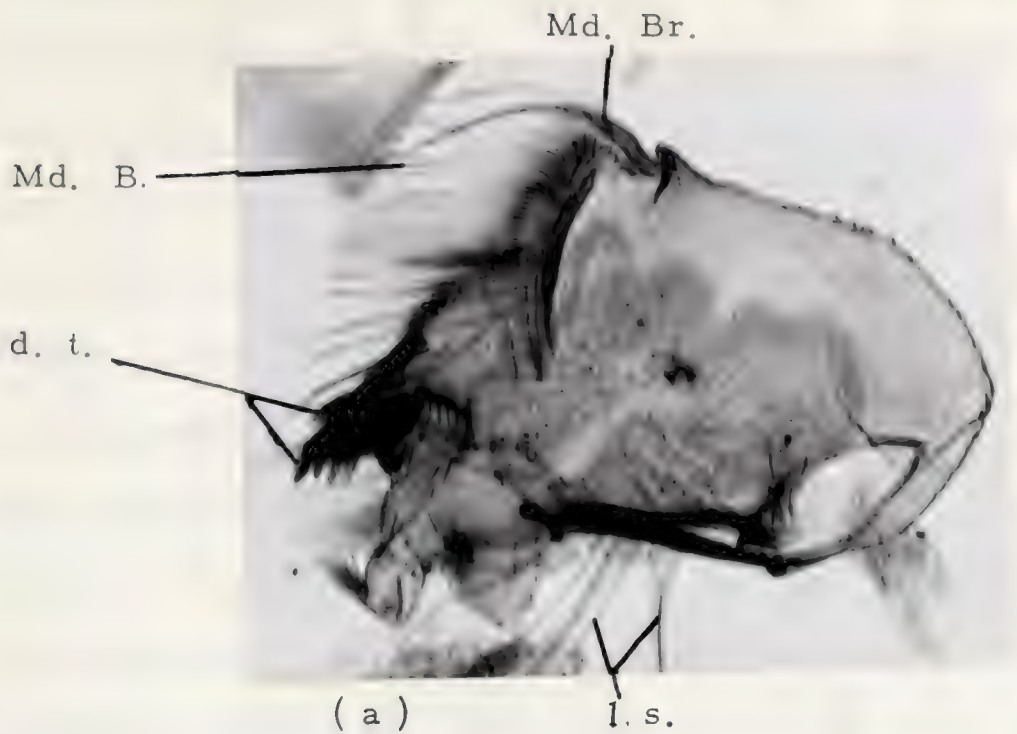


Fig. 8. Dorsal (a) and ventral (b) views of the mandible of *Aedes fitchii* larva. d. t. - dorsal teeth, Md. B. - mandibular brush, Md. Br. - mandibular bristles, Md. c. - mandibular comb, l. s. - long spines.

consists of forty setae; in A. fitchii of fifty-four setae. The number of bristles (Fig. 8, MdBr.) is variable; in A. fitchii two are present and in C. inornata three. When the setae of the mandibular brush and comb are stained with Mallory's their bases stain blue, and thus are soft; the remaining parts stain dark red, and are hard, in the Aedes and the Culiseta browsing species. Blue and light red are the stains in the corresponding structures of the filter-feeding species, Culiseta morsitans and Culex territans. They are thus softer than in the browsing species. The lateral bristles remain brown in all the species examined. All the mandibular bristles and setae in the mandible of Chaoborus americanus stain dark red and some remain brown. These structures are hard.

The number of teeth in A. aegypti (L.), as described by Shalaby, is similar to that in A. fitchii (F. & Y.) and to the other Aedes species that were examined. The number of ventral teeth in C. inornata (Will.) is similar to that found in the Aedes browsing species, but dorsally only three teeth (d. t.) are present in C. inornata (Will.) whereas five are present in the Aedes species. The extent of heavy sclerotization in the tips of the mandibles, mainly the teeth, is approximately the same in C. inornata and the Aedes browsing species. The heavily sclerotized area is relatively smaller in the filter feeders, and it is largely extended in the predators Chaoborus americanus (Johannsen) and Mochlonyx velutinus (Ruthe). These characteristics agree with the characteristics of browsers, filter feeders, and predators that Surtees (1959) discusses. Medially, on the dorso-ventral ridge of the mandible a group of long spines (Fig. 8 (a) l. s.) reaches the anterior part of the pharynx. Schremmer (1949) discusses the function of similar

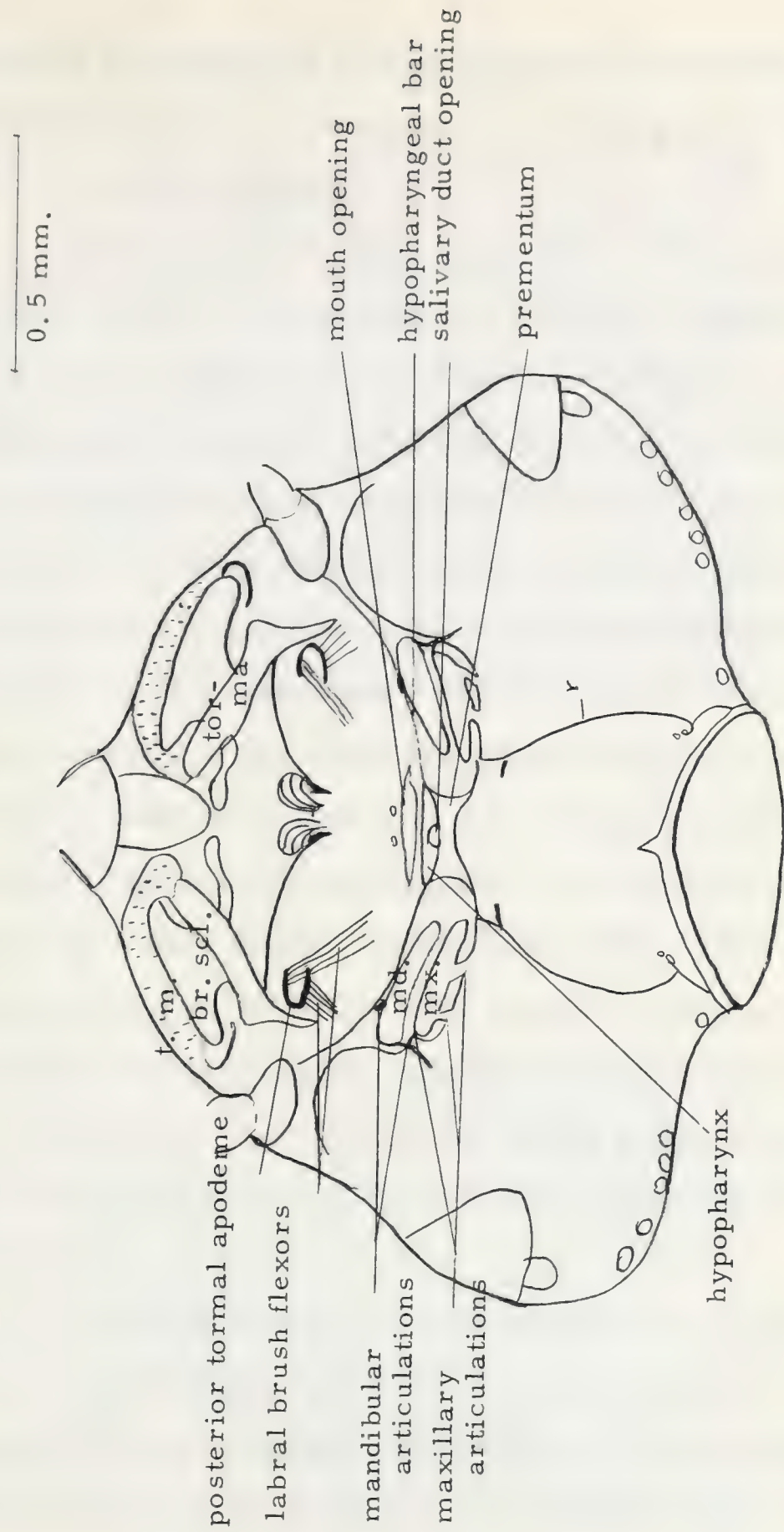


Fig. 9. Ventral view of the head of *Aedes fitchii* larva showing the mandibular and maxillary articulations to the cranium.

spines in the Anopheles maculipennis larval mandible. Anterior and posterior mandibular articulations are indicated in Figs. 8 and 9.

2.3.5. The Maxillae

Each maxilla of Aedes fitchii (Fig. 10) consists of a rectangular flattened lobe which bears a brush of long hairs apically, and a series of three rows of short hairs medially in an area demarcated by a suture on the oral (dorsal) side. Disto-laterally a one-segmented palpus is attached to the maxillary lobe. Below the palpus and about one-half of the main lobe extends a triangular sclerite which is attached to the above mentioned structures and to the postgena by a membrane. This sclerite bears a spine medially. Disto-ventrally on the maxillary palpus are present sclerotized processes which articulate with a postgenal articular process inside the head (Figs. 9 and 10, articulation). The mandible also articulates with the postgena and the maxilla at this point. Two muscles are inserted on the center of the main maxillary lobe; a single strand of muscle originates on the subgena mesally to the posterior tentorial pit; and a double strand originates on the postgena posterior to the eye between the origins of the mandibular abductor muscles (Figs. 2, 3(b)).

To decide what parts of the maxilla of A. fitchii (F. & Y.) larva are homologous with parts of maxillae of other insects, the relation between sclerites and musculature must be considered. It is generally accepted that as Imms (1944) states "...the Mecoptera are the nearest living representatives of ancestors of Diptera..." This view is also expressed by Applegarth (1839), Ferris (1939), Potter (1938), Hinton (1958), and others. We should therefore look

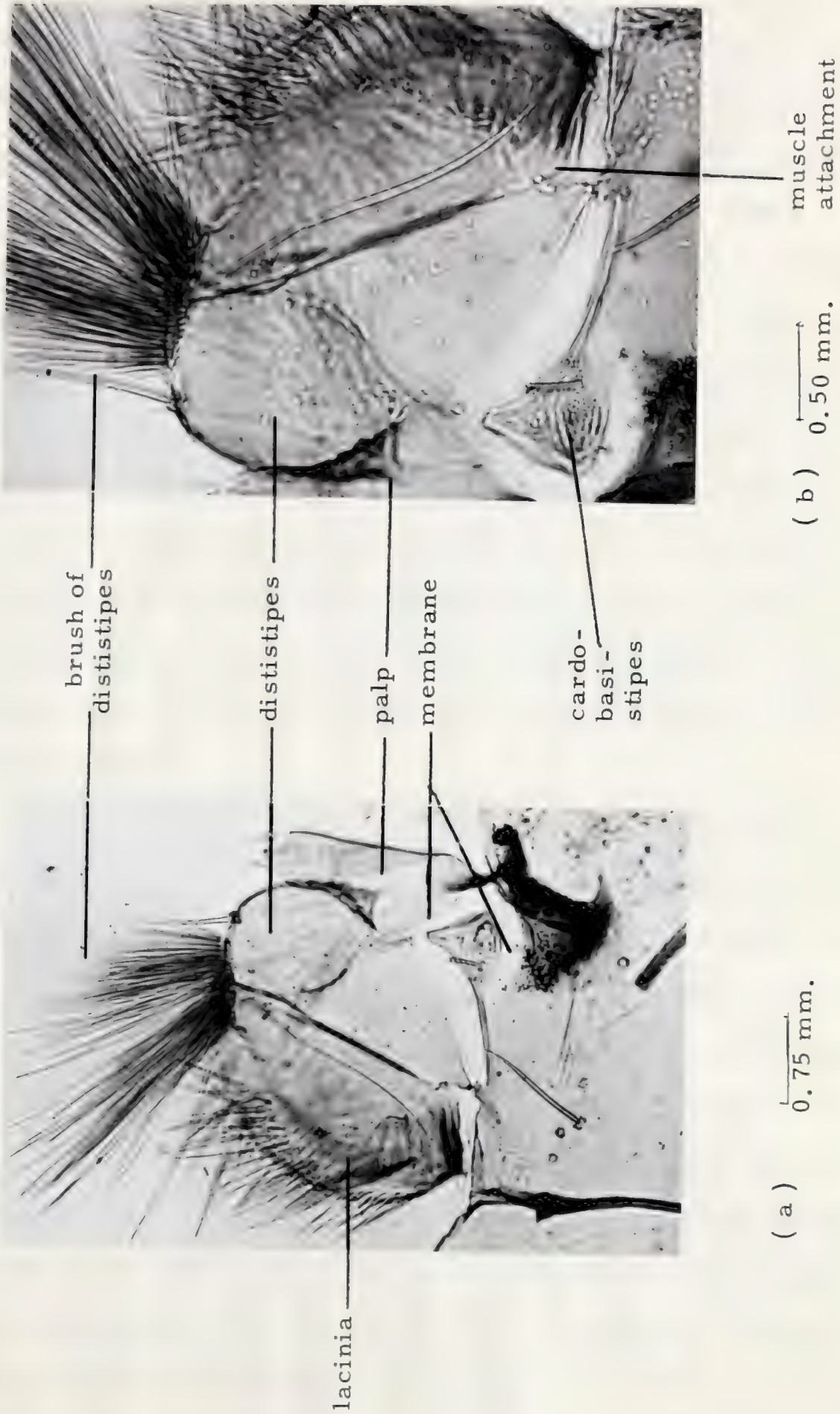


Fig. 10. Dorsal (a) and ventral (b) views of the maxilla of Aedes fitchii larva.

for homologies of the maxilla of the mosquito larva in the Mecoptera and in other members of the suborder Nematocera. The palpus is the only structure on the homology of which all the authors agree. Since the palpus is connected to the base of the main maxillary lobe, and since the palpus in all insects is connected to the stipes, it seems logical to consider this lobe as the stipes. According to Snodgrass (1935) and Das (1937) the stipes can be distinguished by the origin of the muscles of the palpus. However, this criterion does not apply when the palpal muscles are absent as in the mosquito larvae and in the larvae of Tipula and Bibio as described by Das (1937) and Cook (1944). The two muscles that are present in this structure are probably the cranial flexors of the stipes (rather than of the lacinia). The double strand which originates on the postgena is one of these, and the adductor of the stipes which usually originates on the tentorium is the other. In the culicid larva the origin of the latter was shifted to the postgena.

Snodgrass (1935) and Das (1937) hold that the lacinia has a cranial flexor and a stipital flexor and the galea has only stipital flexor in many larval and adult stages of insects. Das also states that in many larval stages the flexor of the galea is absent but when the lacinia is present its muscles are always retained, or at least the cranial flexor is. The same author further states that the cranial flexor of the lacinia plays an important role in the interpretation of the lobes or of the lobe when one of them is absent. In the A. fitchii larval maxilla and in all the other culicid larval maxillae that were examined, no trace was found of the stipital flexors of the lacinia or the galea. Thus, only the cranial flexor of the lacinia is present, and it has

shifted its insertion to the stipes. However, the insertion of this muscle is so close to the median side of the lobe that it is almost on the lacinia; that is, on the bristle-covered area which is demarcated by a suture on the oral side of the maxillary lobe (Fig. 10(b)). Furthermore, this median bristly area serves the function of a lacinia. Therefore it seems reasonable to agree with Shalaby (1957a, 1958) that this part of the maxilla is homologous with the lacinia.

In other insects of the Panorpoid group the following situations exist: in the larva of Panorpa, described by Das (1937), both galea and lacinia are present; in Apterobittacus, described by Applegarth (1939), only the lacinia is present in the larval stage and the galea appears in the pupal stage; in both Tipula, described by Das (1937) and in Bibio, described by Das (1937) and Cook (1944b) only the lacinia is present in the larval stage. The triangular sclerite which is by most authors considered as the palpifer I believe to be at least a partial vestige of the cardo. In the larva of Panorpa as described by Das (1937) the cardo has a relative size, shape and position similar to that in the mosquito larva and it also lacks musculature. In the larvae of each of Apterobittacus, Bibio, and Tipula species the structure named as cardo by the respective authors, Applegarth (1939), Cook (1944), and Das (1937) is proportionately larger than in the larvae of Aedes, Culex and Culiseta. In the former three larvae the so-called cardo extends under the whole of the stipes and the palp. If this structure in each of the mentioned groups is homologous with the triangular sclerite in the mosquito larva then this sclerite must be the cardo and not the palpifer. How-

ever Hinton (1958) points out that the stipes is divided into a basistipes and dististipes in all the Panorpoidea except the more specialized Diptera. The same author further states that failure to recognize the fact that the stipes is subdivided in primitive forms of all recent orders of the Panorpoidea has resulted in the mis-identification of the dististipes as the palpifer. Hinton also states:

"in the Panorpoidea in which the cardo has become fused to the basistipes the combined structure which may be called the cardo-stipes has almost without exception been identified as the cardo and the dististipes as the stipes. For instance, the cardo plus basistipes of Bibio is called the cardo and the dististipes is called the stipes by Imms (1944) and Cook (1949)..."

In the light of Hinton's statements then I consider the triangular sclerite of the mosquito larva maxilla as a homologue of the cardo-basistipes, and the main maxillary lobe as the dististipes plus the lacinia. In addition Hinton mentions that within the Nematocera a fusion of the cardostipes with the dististipes takes place for example in the Culicidae, but he does not specify in what group of the Culicidae. He may be referring to the genus Anopheles, for in that genus a triangular sclerite does not occur below the maxillary palp and the dististipes as in the genera Aedes, Culex, and Culiseta.

Essentially the same structural arrangement of the maxilla was found in all the Aedes, Culex, and some Culiseta larvae that I examined. Some difference from the browsers was found in the shape of the maxillae of Culex territans Walker and Culiseta morsitans (Theo), Aedes canadensis and A. cinereus. Each maxilla in these species is cone-shaped, wide at the base and narrow at the apex where a brush of simple hairs is attached. Each maxilla of most

browsers is similar in shape to that of A. fitchii (F. & Y.). Between the browsers and filter feeders differences occur in the number and length of hairs on the distal end of the dististipes and on the lacinia. In the maxillae of both filter feeders and browsers the apical brush hairs of the dististipes are longer than the lateral hairs of the lacinia, but in the filter feeders all these hairs are proportionately longer than in the browsers. The longest hairs in Culex territans Walk. and in Culiseta morsitans (Theo.) are approximately one and a half times as long as the length of the dististipes; whereas the homologous hairs in A. fitchii and the other Aedes browsers are only approximately as long as the dististipes, and in Culiseta inornata (Will.) as well as in C. impatiens (Walk.) these hairs are half the length of their dististipes. The maxillary brushes of the Aedes browsing species are composed of more hairs than those of the filter feeding species. The maxillae of C. inornata and C. impatiens larvae have brushes consisting of very few hairs, thus resembling the maxillae of the predatory larvae, Mochlonyx velutinus (Ruthe). Another similarity of the maxillae of these two Culiseta species to the predatory larval maxillae is the fusion of the palps with the cardobasistipites.

With Mallory's triple stain the bases of the maxillary brush hairs stain blue and the remaining parts red in the browsing larvae, but the whole hairs stain blue in the filter feeding larvae. Thus the maxillary brushes of the filter feeders are more flexible than those of the browsers. The filter feeders depend on the feeding current for obtaining their food, and the filtering of the food is probably done more easily with flexible hairs than with stiff ones.

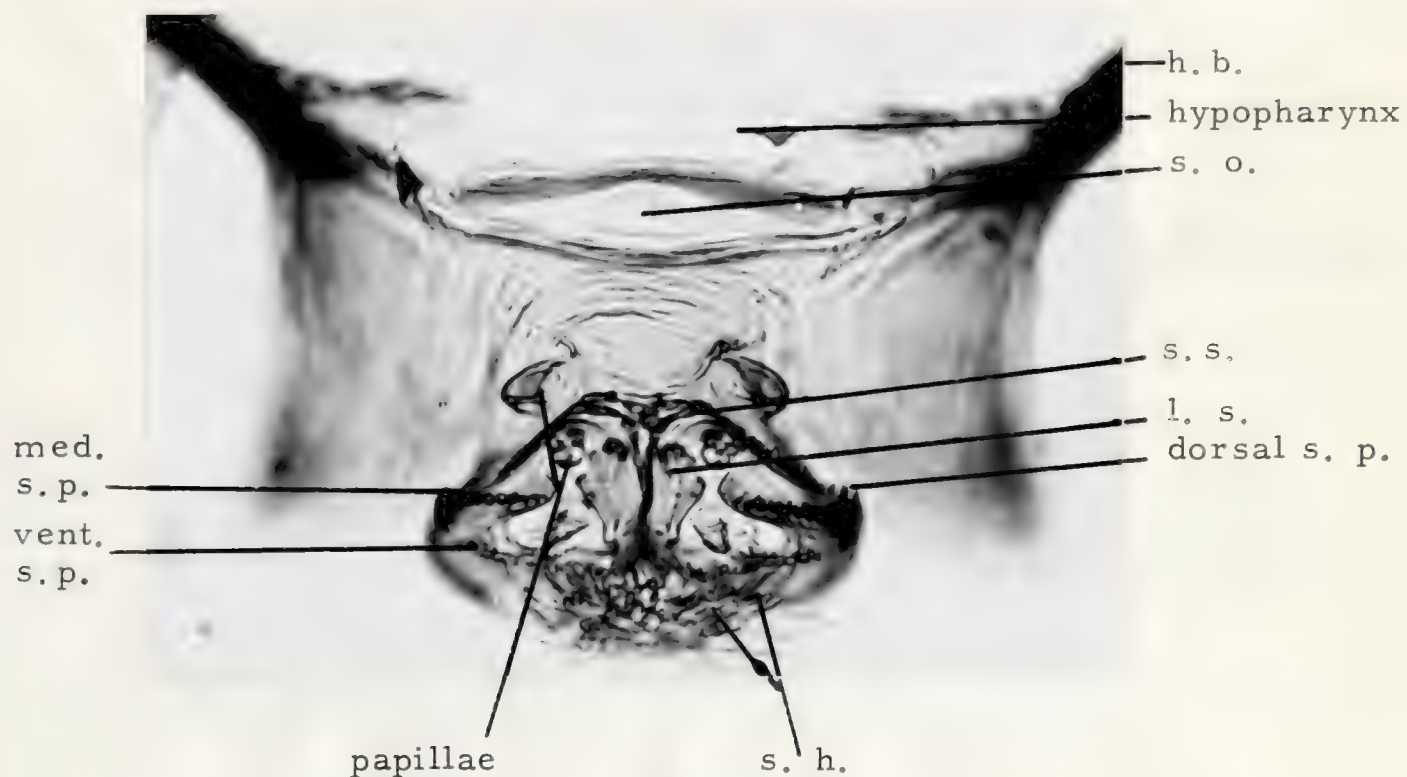
The short medial bristles of the lacinia are arranged in three rows in all the species that I studied; they are more numerous in

A. fitchii and in the other browsers than in C. territans and the other filter feeders. These hairs are longer in A. fitchii and the other Aedes browsers than in C. inornata and C. impatiens. In all the browsers these hairs stain red which indicates their medium stiffness. The hairs of the lacinia of the filter feeders stain blue and thus are soft.

2. 3. 6. The Labium and the Hypopharynx

I consider the labium of the larva of A. fitchii to consist of the prementum and the submentum. This view is in agreement with Cook's (1944 b) interpretation. The prementum (Fig. 3(a), pm.) is a rectangular membranous area bearing a series of serrated sclerites and papillae, and is situated vertically between the hypopharynx and the mouth opening dorsally, and the triangular serrated submental plate ventrally (Figs. 3 (a), 9, 11, sm.).

Dorso-ventrally two long sclerites (Fig. 11, l. s.) extend through the center of the prementum and dorsally terminate in front of six small serrated sclerites (Fig. 11, s. s.) which project horizontally from the membranous base. On the lateral sides of the membrane three serrated plates (s.p.) are situated horizontally. These three plates are connected to each other, and dorsally they are connected with the small central serrated sclerites (Fig. 11). Each of the three plates has a different number of serrations, and these numbers vary in different species. In A. fitchii the dorsal plate bears four serrations most commonly (five specimens were examined for this), the median plate bears nine serrations, and the ventral plate five. Six larvae of each of two closely related species, Aedes hexodontus and A. punctor were also examined, and the averages of the numbers of serrations were found to be as follows: dorsal plate (Fig. 11, dorsal s.p.) - 5 serrations in A. hexodontus, 4 in A. punctor; median plate



0.50 mm.

Fig. 11. Dorsal view of the prementum and the hypopharynx of *Aedes fitchii* larva. Abbreviations: h. b. - hypopharyngeal bar; l. s. - longitudinal sclerite; med. s. p. - median serrated plate; s. h. - serrated hairs; s. o. - salivary duct opening; s. s. - serrated sclerite; vent. s. p. - ventral serrated plate.

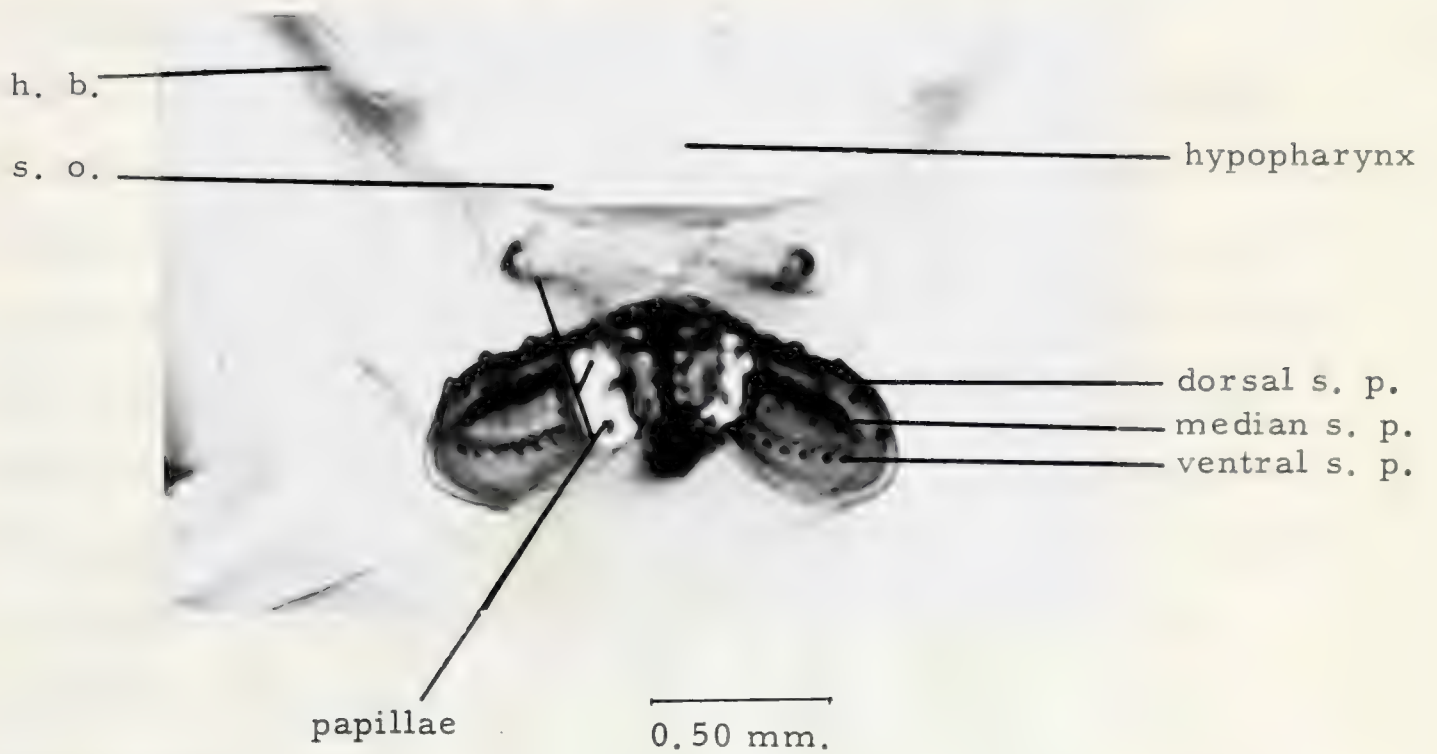


Fig. 12. Dorsal view of the prementum and the hypopharynx of Culex territans larva. Abbreviations are the same as in Fig. 11.

(Fig. 11, median s.p.) - 6 serrations in A. hexodontus, 9 in A. punctor; ventral plate (Fig. 11, ventral s.p.) - 6 serrations in A. hexodontus ,10 in A. punctor. This may be a useful taxonomic character for separating closely related species. Considerable care is required in preparing the slides if the serrated plates are to be seen clearly.

The serrated plates in all the species of Aedes, Culiseta, and Culex that were examined stain light red basally and dark red to orange distally. This means that the plates are quite hard, but this is understandable because the mandibular teeth which are of similar hardness strike against these plates. In the Aedes species a group of broad, apically serrated hairs originates on the mid-ventral side of the premental lobe (Fig. 11, s.h.). Broad, but not apically serrated hairs in the same position are present in the Culiseta and the Culex species that were examined. Large numbers of these hairs are present in the Aedes and Culiseta species, but very few are present in the Culex species. In all the species examined these hairs stained medium red with Mallory's triple stain.

On the premental lobe laterally, between the central and the lateral serrated plates four small papilla-like structures are present in all the species of Aedes, Culiseta, and Culex that were examined (Figs. 11, 12, papillae). The most dorsal processes are double on each side, and more ventrally two arise singly on each side. Two similar papilla-like processes are present in the membrane dorsally between the serrated plates and the salivary duct opening (Figs. 11, 12, s.o.). In all the species that were examined the papillary structures stained red, and the basal membranes stained light blue. In feeding larvae food was often seen collected in the spaces between the papillae and the serrated plates.

It is difficult to homologize the structures of the labium, but since a pair of muscles attaches the rectangular lobe to the subgena medial to the posterior tentorial pits (Fig. 2), these muscles are considered as the premental muscles by Cook (1944 b, 1949), Snodgrass (1959), and some others. The lobe is therefore considered as the prementum, and I agree with Cook's interpretation of this. Snodgrass, however, refers to this lobe as the labial plate, not only as the prementum. The premental membrane is dorsally suspended from the hypopharyngeal bars (Figs. 11, 12, h. b). A light suture continues between these bars and dorsally of the premental membrane, thus demarcating an oval membranous hypopharyngeal area above the prementum (Figs. 11, 12, hypoph.). The opening of the salivary duct is located between the premental and the hypopharyngeal lobes (Figs. 11, 12, s.o.).

The triangular serrated sclerite below the prementum has been variously named (Table 1). I agree with Cook (1944 b, 1949) that it represents the submentum. Snodgrass (1959) believes it to be an extension of the subgena. My main reason for disagreeing with Snodgrass is the fact that this sclerite articulates with the subgena, and therefore is unlikely to be an extension of it. With Mallory's triple stain this sclerite stains orange basally and remains dark brown apically in all the Aedes, Culex, and Culiseta larvae that were examined. It is thus a very hard structure, and it is not easily penetrated by KOH so that it would accept the stain. The serrations on it are rather constant in the species examined. In A. fitchii 16 out of 20 specimens had submenta with 21 serrations, one had 20, one 19, and two had 18 serrations. It is possible, however, that all of these larvae may not have been mature fourth instars, and therefore they

lacked one, two, or three serrations . Table 2 shows the means of numbers of submental serrations in the various species that were examined.

The lightly sclerotized fringe of hairs (Figs. 2, 3 (a) , aul.) which is attached to the submentum ventrally I consider as a part of the submentum since it is very intimately connected with this structure. Cook (1944 b) calls it the "aulaeum , " a curtain. With Mallory's stain this fringe stains light orange ; it is thus hard.

2. 3. 7. The Pharynx

The pharyngeal structure and musculature of A. fitchii (Fig. 13) and C. inornata larvae are similar to the structure described by Cook (1944 b) in Theobaldia incidens (= Culiseta incidens). The large dorsal and ventral sclerites stain light orange in all the Aedes, Culex and Culiseta larvae that were examined. The lateral dorsal hairs stain light red, and the inner filtering hairs stain light blue in most species . Therefore these hairs are flexible. Schremmer (1949) described the filtering function of the pharyngeal hairs in the Anopheles maculipennis larva.

2. 3. 8. Conclusions and Discussion

The following conclusions have been drawn on the nomenclature and homologies of the mouthparts of mosquito larvae:

The largest dorsal head sclerite is the frontoclypeus, and the fronto clypeal suture is degenerate. The labrum consists of a narrow sclerite dorsally, and ventrally it bears specialized feeding organs. In the non-predatory culicine larvae these feeding organs consist of two lateral brushes and a median brush. In the filter feeding species the lateral labral brushes consist of long, simple hairs; in the browsing species the lateral labral brushes contain serrated and

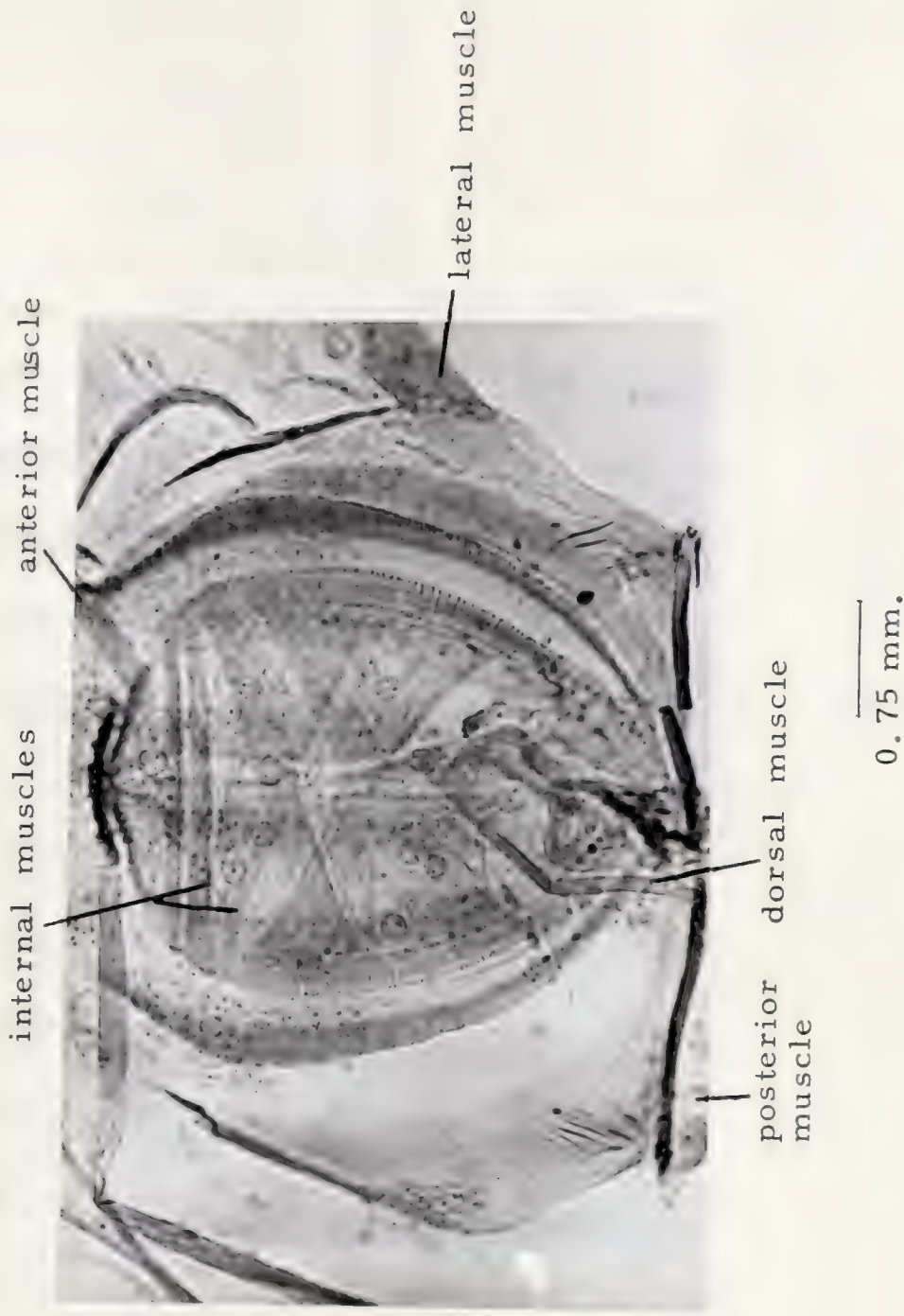


Fig. 13. Dorsal half of pharynx with its musculature of Aedes fitchii larva.

Table 2. The number of serrations present on the submentum
of mosquito larvae that were studied.

Species	No. of submental serrations		Species	No. of submental serrations	
<u>Aedes</u> species			<u>Culiseta</u> species		
<u>campestris</u>	27.0	(1) *	<u>impatiens</u>	25.0	(1)
<u>canadensis</u>	20.0	(1)	<u>incidens</u>	18.0	(1)
<u>cinereus</u>	25.0	(1)	<u>inornata</u>	23.9 $\pm$ 3.2	(17)
<u>excrucians</u>	20.5	(2)	<u>morsitans</u>	19.0	(2)
<u>fitchii</u>	18.8 $\pm$ 1.9	(20)	<u>Culex</u> species		
<u>hexodontus</u>	24.6 $\pm$ 1.2	(5)	<u>pipens</u>	21.0	(2)
<u>implicatus</u>	18.0	(1)	<u>tarsalis</u>	13.0	(2)
<u>increpitus</u>	25.0	(1)	<u>territans</u>	13.0	(2)
<u>impiger</u>	20.5 $\pm$ 0.3	(4)			
<u>pionips</u>	24.0	(2)			
<u>punctor</u>	27.0 $\pm$ 1.9	(6)			
<u>riparius</u>	23.6 $\pm$ 1.4	(5)			
<u>sticticus</u>	21.6 $\pm$ 0.4	(3)			
<u>stimulans</u>	28.0	(1)			
<u>vexans</u>	26.0 $\pm$ 0.7	(5)			

* average $\pm$ S. D. of the mean (where applicable);
number of specimens examined in parentheses.

and unserrated hairs which are shorter than the brush hairs of the filter feeders. In the predatory Chaoborus and Mochlonyx larvae the reduced labral areas bear small numbers of simple hairs as described by Schremmer (1950) and Cook (1956).

The epipharynx and the mandibles. I agree with other authors on the homology and nomenclature of these structures. In the post-epipharyngeal area of A. fitchii (F. & Y.) three muscle fascicles are present whereas in Theobaldia incidens (Thomson) (= Culiseta incidens (Thomson)), described by Cook (1944 b), only two muscle strands are present in this area.

The maxillae. A modified nomenclature is proposed for the parts of the maxilla of the Aedes, Culiseta and Culex larvae that were studied. The main lobe of the maxilla I consider as the dististipes. The medial portion of this structure, bearing three rows of setae and separated from the main lobe by a suture on the dorsal side, I consider as the lacinia. No vestiges of the galea are apparent. On the lateral side of the dististipes a one segmented palpus is attached. The triangular sclerite which is situated below the palpus and below approximately half of the dististipes I consider to be the cardobasistipes. Interesting maxillary structures are found in the genus Culiseta. In Culiseta morsitans, as in the Culex filter feeders and the Aedes browsers, the triangular sclerite is separated from the palpus; but in the C. impatiens and C. inornata, this triangular sclerite is fused with the maxillary palp as in the maxilla of the predatory larva Mochlonyx. In Chaoborus americanus (Johannsen) the main lobe of the maxilla consists of the cardostipes, but this lobe Cook (1956) calls the stipes. In arriving at the conclusions in this

section various works on the morphology of larval mouthparts of mosquitoes, other Nematocera, Panorpa, and other Mecoptera were studied. Finally Hinton's (1958) criteria for the homologies of mouthparts in the Panorpoid group of insects were followed.

The labium and hypopharynx. I agree with Cook's (1944 b, 1949) conclusions on the homologies of these structures. Essentially, the labium in the Aedes, Culiseta, and Culex larvae which I examined consists of a reduced prementum and submentum. Hinton (1958) states that in the Zeugloptera, Trichoptera, and Lepidoptera the oral (dorsal) surface of the prementum probably represents the hypopharynx, and the combined structure may be called the premento-hypopharyngeal lobe. In the culicine larvae that I examined a weak suture is present between the prementum and the area dorsad of it on which the salivary duct opens, therefore the area between the mouth opening and the prementum I consider as the hypopharynx. Snodgrass (1959) considers as labium-hypopharynx the structures which I call the prementum and the hypopharynx. In all the species that were examined in the course of this work the salivary duct opening was found on the hypopharynx, and not in the center of the prementum as Christophers (1960) indicates in Aedes aegypti.

The triangular serrated sclerotized structure (Fig. 2, sm.) , immediately ventral to the prementum I consider to be homologous with the submentum, and the fringed plate which is attached to it I consider as a lobe of the same structure since these two structures are intimately connected with each other in all the larvae that I examined. Snodgrass regards the triangular serrated plate as a part of the cranial wall, an extension of the subgena. This interpretation does not seem

very satisfactory since the triangular sclerite articulates ventrally with the subgena, and generally the submentum of insects does articulate with the ventral part of the cranium (Snodgrass 1935). The same author (1959), however does not mention that the triangular structure articulates with the subgena; he states that it is continuous with the subgena as in the heads of Chironomus larvae. It seems that Snodgrass did not examine the subgenal and the labial portions of the mosquito larval head very carefully.

Shalaby's (1957 d) interpretation of the triangular sclerite as the paraglossa, and the interpretation of the aulacum as the glossa is unique, and seems unreasonable. The areas which I consider as the prementum and the hypopharynx Shalaby regards as the hypopharynx. Medio-laterally on the premental lobe a pair of muscles is inserted. These muscles originate on the ventral sclerite of the head which Shalaby considers as the submentum and which I regard as the subgena. It is difficult to agree with Shalaby's interpretation of the labium and the hypopharynx for the following reasons: Firstly, as far as is known, the hypopharynx in insects is not connected with the paraglossa, but in the mosquito larva, in Shalaby's interpretation the "hypopharynx" is firmly attached to the "paraglossa". Secondly, other authorities on the morphology of insect larvae (Cook 1944 , 1949; Hinton 1958) state that the retractor muscles of hypopharynx are absent in Diptera. Thirdly, when the retractors of the hypopharynx are present they arise on the postoccipital ridge in the Trichoptera, and on the transverse tentorial bridge in the Lepidoptera (Hinton 1958), but not on the "submentum" where these muscles originate in the mosquito larva according to Shalaby's interpretation.

In the above interpretation of the homologies of the mouthparts of mosquito larvae, origins of muscles and relative positions of structures are considered. Cook (1944 a) and Ferris (1943) express the importance of muscle origins in the homologizing of structures.

It is difficult to decide on the homologies of degenerate structures such as are the structures of the mouthparts of mosquito larvae, especially those of the maxilla and the labium. Very few muscles which could serve as guides to homology are present, and this is partly why disagreements exist among the various morphologists who study mosquito larval mouthparts. Every worker in this field seems to think that his guess is somewhat better than the guesses of the others. Ferris (1948) postulates the following principle : "...that evolutionary changes are first to be accounted for by modifications of pre-existing structures, or by loss of pre-existing structures; ... Only after these possibilities have been exhausted will we assume that a completely new structure has been developed...." This principle can be applied to the mosquito larvae and to the larvae of other primitive Nematocera when we compare them with the larvae of *Panorpoidea* from which group the *Diptera* are believed to be derived. In the mosquito larvae noticeable modification from *Panorpa* is seen in the labrum and in the mandibular teeth. Losses and fusions of pre-existing structures are evident in the mosquito larval maxilla and the labium.

A difference was found in the hardness and flexibility of the cuticle of the mouthparts of the filter feeding, browsing, and predatory mosquito larvae. Essentially, the mouthparts of the filter feeders are rather soft except for the labral brush hairs and the mandibular teeth; the mouthparts of the browsers are harder than those of the

filter feeders; and the mouthparts of the predatory larvae are the hardest of all, especially their mandibles which are highly sclerotized.

The tips of the simple labral brush hairs of the filter feeding and browsing larvae are softer than the main parts of the hairs. The labral brush hairs of these groups of larvae are much harder than they appear to be at first sight, since they will not stain with Mallory's triple stain until they are boiled in a KOH solution which must not be less concentrated than 8 %. It was interesting to find that the serrated ends of the lateral labral brush hairs of the browsing larvae stain blue and thus are soft combs rather than hard ones as they may be expected to be when their function is considered. Since they are soft it is probable that when they comb surfaces of objects they detach mainly soft particles and direct them towards the mouth. This, as far as is known, is the first report of the relative cuticular hardness of the mosquito larval mouthparts which has been found by differential staining.

It is evident from the observations in this work that certain similarities are found in the mouthparts of the three types of larvae that were here examined. The serial row attachment of the labral brush hairs to their respective bars is similar in the browsing and the filter feeding larvae. Christophers (1960) notes that the hair attachment is also similar in the larvae of a Culex species and Aedes aegypti that he examined. Additional information on the lateral labral brush attachments is given in the present work.

In Table 3 it is indicated that a reduction occurs in the number of hairs or bristles on the various mouthparts; this trend runs from the filter feeders to the predators. In the same series an increase in the sclerotization of the mandibular teeth is evident.

Table 3. List of some similarities and differences in the mouthparts of Albertan species of filter feeding, browsing and predatory mosquito larvae.

SPECIES	MOUTHPARTS					
	Labral brush hairs	Maxillary hairs	Labial (premental) hairs	Sclerotization	Mandible Tooth Plane of action	
Filter feeders <u>Culiseta morsitans</u>	No. Length Quality many long simple thin	No. Length many very long	No. Length few short	moderate	slight	
<u>Culex territans</u>	many long simple thin	many very long	few short	moderate	slight	
Intermediate <u>Aedes cinereus</u>	med. simple thin	very many long	many long	moderate	heavy	nearly horizontal
Browsers <u>Aedes fitchii</u>	med. ser-rated thick	very many long	many long	moderate	heavy	
<u>Culiseta inornata</u>	med. ser-rated thick	few short	many long	moderate	heavy	
Predators <u>Mochlonyx velutinus</u>	few short serrated wide thick	very few very short	many mostly long	slight	very heavy	
<u>Chaoborus americanus</u>	very few serrated wide thick	absent	very few short	none	very heavy	antero-ventral

It is interesting to find the same genus represented by filter feeding (Culiseta morsitans) and browsing larvae (C. inornata and C. impatiens) whose mouthparts are tending towards the predatory type. Most of the Aedes species that were studied are browsers, but the larvae of A. cinereus Meig. and C. canadensis (Theo.) lack serrations on their labral brushes, have more weakly sclerotized mandibular teeth than the other Aedes species, and their maxillae are similar to those of the filter feeding species. Thus morphologically these species seem to be intermediate between the filter feeders and the browsers.

From Table 3 it is also evident that the plane of action of the mandibles in the predatory larvae tends towards that of the longitudinal axis of the body which is a character common among the larvae of the higher flies according to Cook (1949).

3.0 FUNCTION OF THE MOUTHPARTS OF MOSQUITO LARVAE

3.1. INTRODUCTION

The object of the investigations in this part of the work was to find how the structures studied in the previous section are used. I shall attempt to show in this section that a correlation exists between the structure and function of the mouthparts of mosquito larvae.

3.2. PROCEDURES

The movements of mouthparts of mosquito larvae and actions resulting from these movements were studied in three types of situations: 1. Larval behavior (mostly Aedes) was observed in the muskeg pools in the Flatbush area (100 miles North of Edmonton) mainly in the summer of 1960 and some in 1961. 2. Most observations were made on active larvae in the laboratory. After being collected the larvae were kept in half quart glass jars, and in order to retard their development in hot weather, when not observed they were kept in the refrigerator set at 40° F. The larvae were observed in groups and individually in the glass jars and some details of movements of their mouthparts were seen with the aid of a 10x hand lens. Individual larvae were placed in small vials and their mouthparts were observed from the side with the hand lens. 3. A 30% solution of Methocel was used to slow down the motions of the mouthparts so that details of their actions could be studied. Two species of mosquitoes, Aedes aegypti (L.) and Culiseta inornata (Will) were reared in the laboratory. Many other species, mainly those of the genus Aedes were collected in the field, mostly near Flatbush, Alberta. Several species of Aedes were also collected in the

vicinity of Hastings Lake (60 miles S.E. of Edmonton), some were collected at Banff, Alberta, some at Seebe, Alberta. Culiseta inornata and C. impatiens were obtained from a pool two miles N. W. of Edmonton. The specimens were identified with the help of the keys of Rempel (1953) and Carpenter and LaCasse (1955).

Since the mouthparts are ventral it was most desirable to observe them from the ventral side, and three methods were employed for doing this. In all the methods the larva with food was placed in the same type of container which was constructed by cutting an inch long piece of a plastic vial of one inch diameter, and gluing it to a microscope slide which thus formed the bottom. The container was filled with either pond water or distilled water if no pond water was available. One or two larvae were placed in it, but mostly only one larva was studied at a time.

By means of two concave mirrors light from two intensity lamps was directed onto the larva through the bottom of the container. An image of the ventral surface of the larva was reflected by two plane mirrors to the microscope (Fig. 14). The mouthpart movements were fairly well seen in this apparatus. The movements were most clearly seen at magnifications of six and twelve diameters. More detail was seen under 25X and 50X, but the images were rather blurred, especially at 50X. Another method of observing the larval mouthparts was by turning the body and eye pieces of the binocular microscope up-side-down and focusing on the larva above the microscope. The best focus was obtained by this method which was used most often. Fluorescent light from above and light from below were used separately and in

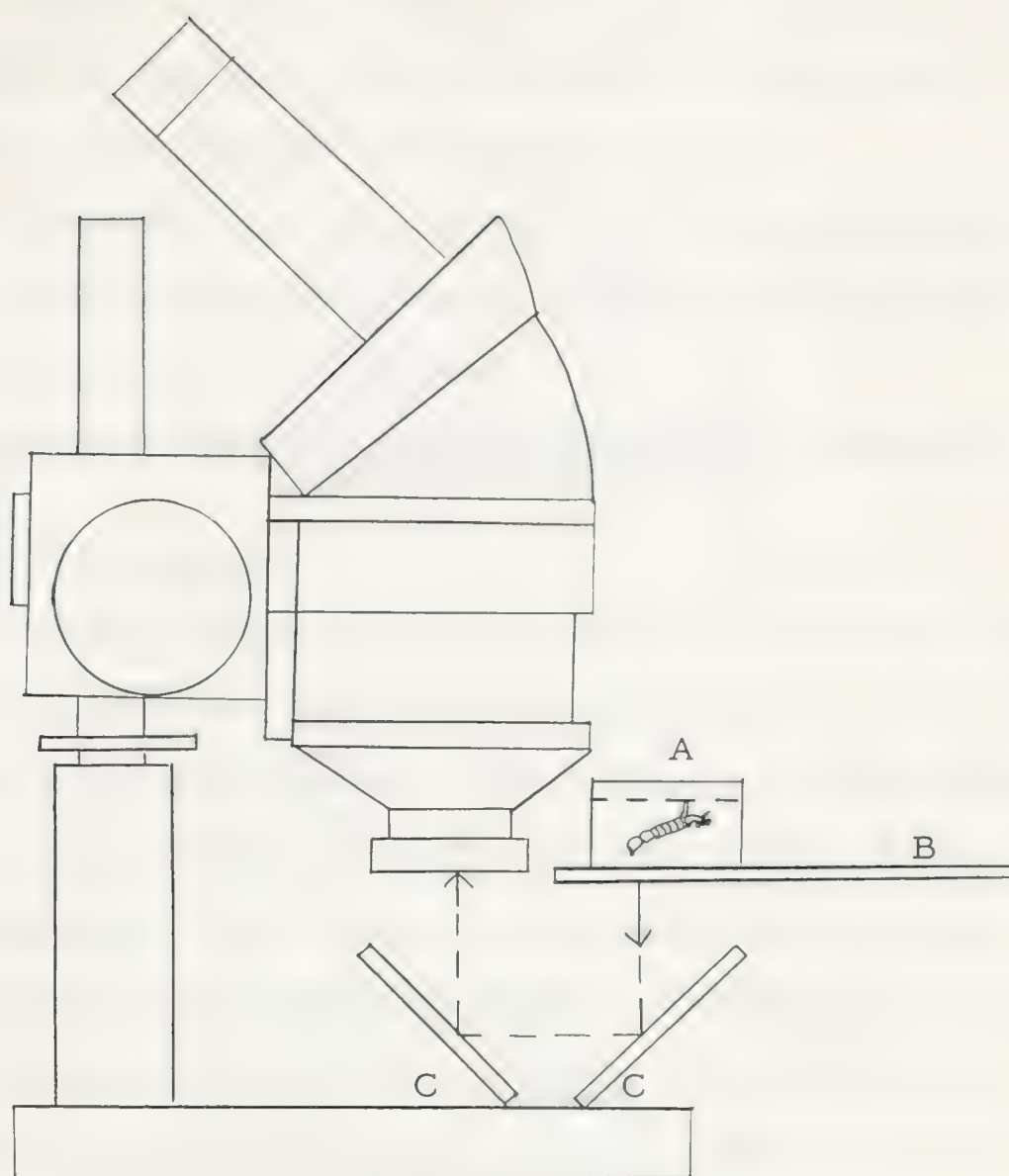


Fig. 14. Apparatus used in studying the action of the mouthparts of mosquito larvae. A - container in which larvae were placed; B - microscope slide; C - plane mirrors inclined at 45°

combination. A more convenient method of observing the activity of larval mouthparts was by using a metalurgical binocular microscope with the stage above the objective lens. In this method it was possible to have the light coming only from above.

Particles of activated charcoal and methyl red powder were placed in the containers with the larvae to show the directions of the currents set up by the mouthparts.

3.3. OBSERVATIONS OF THE MOUTHPARTS OF MOSQUITO LARVAE IN ACTION

3.3.1. Browsers

The main feeding current is produced by the lateral labral brushes, and it is directed toward the epipharynx and the mouth by the central labral brushes. When creating a current the lateral labral brushes vibrate anteroposteriorly and towards the median line of the head. Fig. 15 shows the main lines of action of the labral brushes and the other mouthparts. The brushes can vibrate for various periods of time; in A. aegypti this may be as long as two and a half minutes without stopping. Then they usually stop for five to ten seconds and then resume the beating again. However, in most larvae the brushes usually vibrate for twenty to fifty seconds, stop for five to ten seconds, and move again. In Culiseta inornata and in the Aedes browsing species the duration of currents is shorter. In Table 4 rates of movement for C. inornata (Will.) and A. aegypti (L.) are indicated. This table shows the means of numbers of movements of the lateral labral brushes averaged for five minute intervals, and an average duration of each series of continuous movements. Thus in the

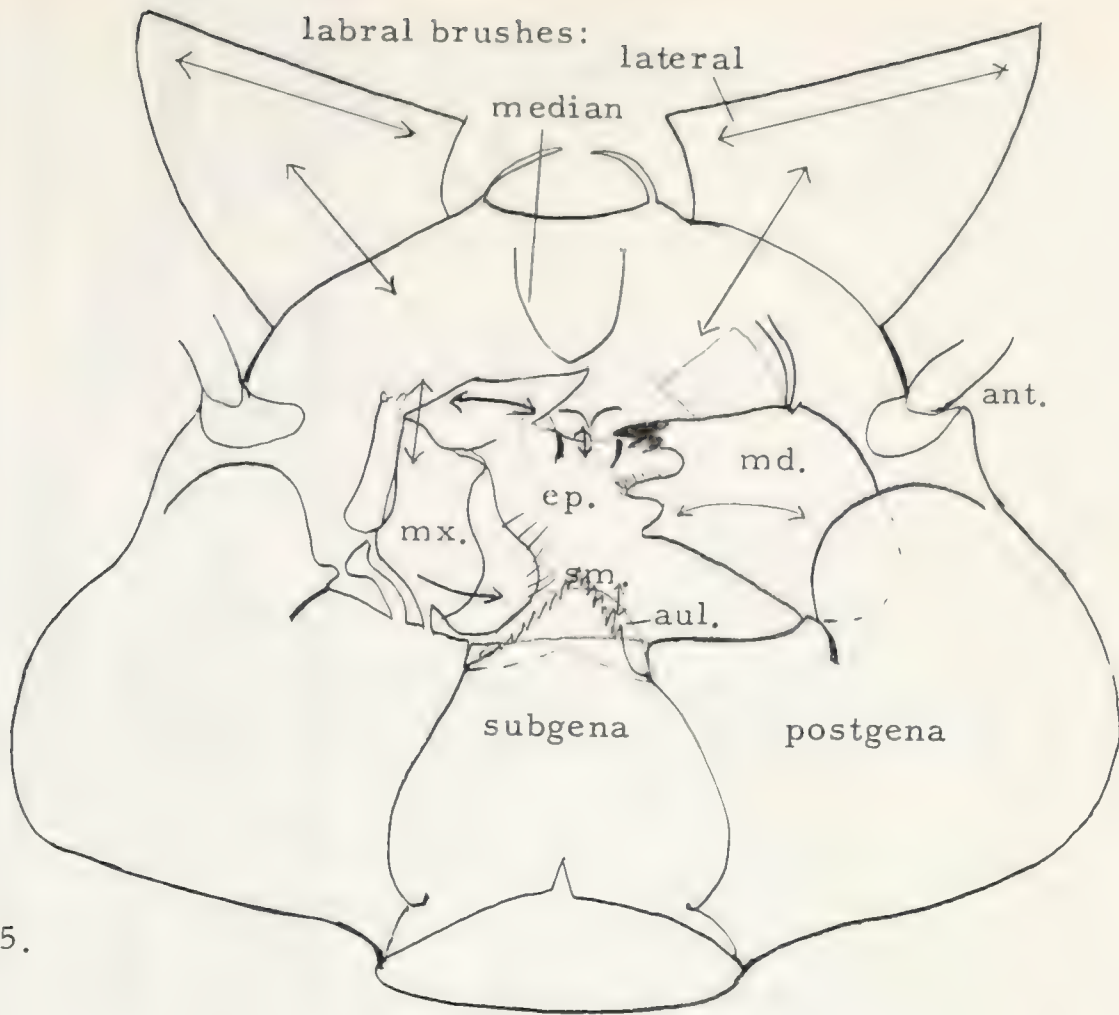


Fig. 15.

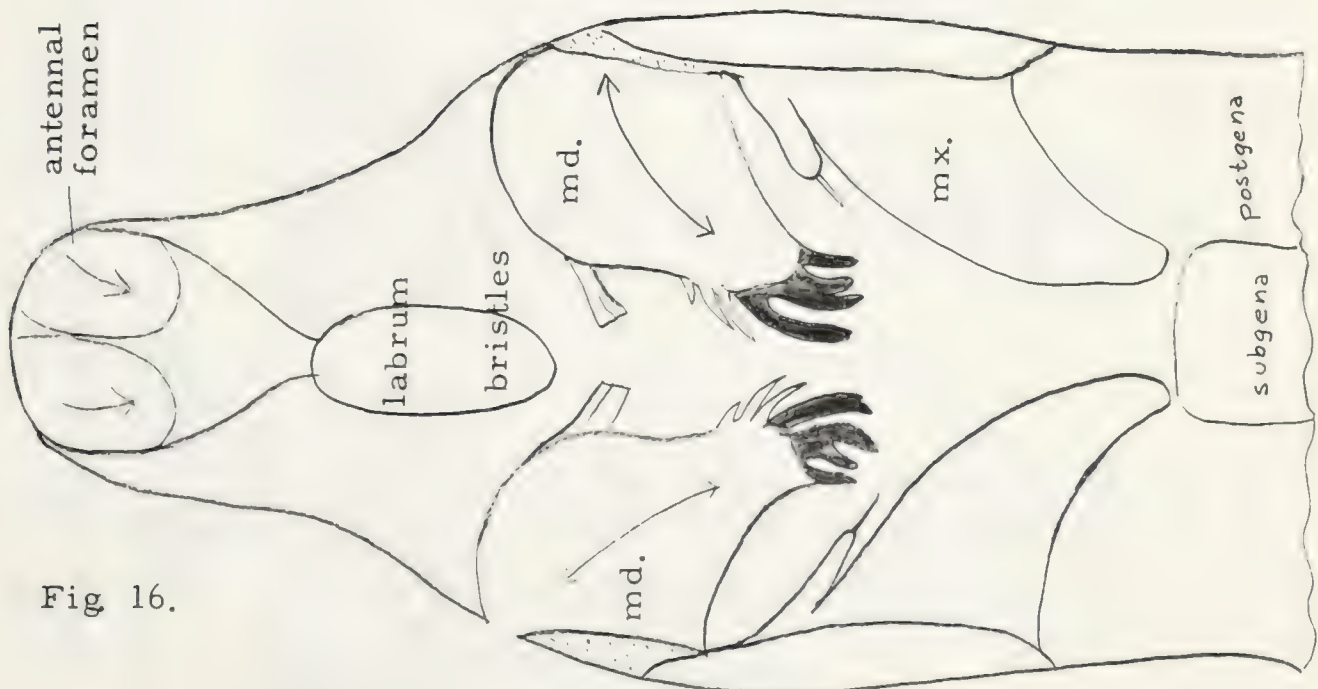


Fig. 16.

Fig. 15. & 16. Main lines of action of the mouthparts of the larvae of *Aedes*, *Culex* and *Culiseta* (Fig. 15) and *Chaoborus* larvae (Fig. 16.)

Table 4. Rates of movement of the lateral labral brushes of C. inornata (Will) and A. aegypti (L.) larvae.

Time (min) from begin- ning of obser- vation period	<u>Aedes aegypti</u>		<u>Culiseta inornata</u>			
	<u>4th instar</u>		<u>2nd and 3rd instars</u>		<u>4th instar</u>	
	3 larvae		2 larvae of each instar		3 larvae	
	Average No. of movements per second	Average dura- tion each series of movements (in seconds)	Average No. of movements per second	Average dura- tion each series of movements (in seconds)	Average No. of movements per second	Average dura- tion each series of movements (in seconds)
5th min.	1.7	28.5	2.6	11.0	2.0	30.0
10th	2.7	17.7	3.0	11.0	3.3	13.0
15th	3.3	37.0	2.4	62.5	1.8	8.0
20th	3.1	35.5	3.1	24.0	1.8	7.0
25th	3.4	65.0	2.8	16.4	1.8	7.0
30th	3.5	27.0	2.6	31.0	1.3	4.0
35th	4.0	25.0	3.0	11.7		
40th	3.7	36.4	2.8	12.0		
45th	3.6	68.0	2.1	6.0		
50th	4.5	32.5	4.6	13.7		
55th	3.7	61.0	3.2	12.5		
60th	3.5	40.3	3.4	16.6		

first five minutes of an hour long observation period the mean number of labral brush movements of 3 fourth instar A. aegypti larvae was 1.7 times per second and the mean duration of each series of movements was 28.5 seconds. Table 5 shows activity of the individual 4th instar C. inornata larvae each of which was observed for 30 minutes. During each 30 minute period the activity of the whole body and the mouthparts was observed, and a percentage of each observable activity was calculated. Thus 22.5% of 30 minutes larva No. 1 was observed with its labral brushes extended, 17.3% of that time with the brushes retracted, and 7.1% of the time the brushes, the mandibles and the maxillae moved together in browsing activities. These various activities of the mouthparts occurred while the remainder of the body was either stationary or moving.

Feeding and locomotory activities of approximately fifty C. inornata (Will) larvae were observed individually for various periods of time throughout the period of study, and many more were observed in group behavior. Much similarity was noticed in the pattern of behavior of the various individuals, and almost any larva could be chosen to represent the common sequence of activities. The following is a summary of the activities of a 4th instar C. inornata (Will.) actively browsing larva (larva No. 6 in Table 5), observed for twenty minutes at a magnification of 25X. The container was filled with pond water.

Table 5. Activity of seven 4th instar larvae of *Culiseta inornata* (Will.). Each larva was individually observed for 30 minutes. Every number represents the percentage of time during which a larva was engaged in a particular activity.

Feeding activity				Activity of larvae		
Extended	Labral brushes		* Indeterminate	* Indeterminate		
	Retracted	Browsing (all mouth- parts active)		Stationary	Moving	
22.5%	17.3%	7.1%	53.1%	25.3%	27.1%	47.6%
10.0	3.0	4.0	83.0	13.0	12.0	75.0
20.0	7.5	7.5	65.0	40.0	25.0	35.0
10.0	0.0	6.0	84.0	10.0	13.0	77.0
11.4	2.9	31.4	54.3	28.6	25.8	45.6
12.5	4.1	64.7	18.7	8.4	10.4	81.2
11.4	14.0	14.3	60.3	6.6	51.4	42.0

* In this category are included activities of larvae and their mouthparts when the larvae were out of the field of view, out of focus, when they moved very rapidly, and while the observer looked at the timer.

The first five minute period:

During the first minute the larva was stationary; it was suspended from the water-surface film and had its labral brushes extended. For the next ten seconds the labral brushes, the maxillae, and the mandibles participated in creating a current, then for ten seconds a period of rest followed for the retracted mouthparts and the whole body. During the first five-minute period such a succession of currents in which all the mouthparts participated was produced four times, and each time the labral brushes moved about fifteen times. The mandibles and the maxillary brushes also moved approximately as many times as the labral brushes.

The Second five-minute period:

The larva browsed on a filamentous piece of plant for ten seconds. The piece of plant was enclosed by the labral brushes and the mandibular teeth struck it. Then the larva moved on to another piece of plant (a chickweed leaf) and browsed on its edges for eighteen seconds. The edges of the tissue were held by the median bristles of the lateral labral brushes while the more lateral bristles of the brushes produced a current which moved the larva forwards along the leaf. The mandibular teeth struck the tissue. Then the tissue was left and further currents were produced by the mouthparts. Pieces of debris passed into one succession of currents which was produced continuously for approximately twenty seconds. Mandibular teeth seemed to

chop off small pieces of decayed material some of which went into the mouth and the remainder moved out with the current. Again a piece of plant tissue was browsed upon, and it was propelled posteriorly. When one end of the plant was at the submentum the aulacum clung to it for a few seconds, but with the subsequent current the tissue was forced posteriorly and towards the bottom of the container.

During the next ten minutes continuous movements of the mouthparts occurred fifteen times, each time the current being produced for approximately fifteen seconds. The activities of the larva were similar to those indicated above.

The amount of brush movement and body movement varies among larvae of different ages and different species. Thus fourth instar larvae are generally more sluggish than younger larvae, and fourth instar Aedes fitchii (F. & Y.) and Culiseta inornata (Will) larvae are more sluggish than the corresponding instar larvae of A. aegypti (Table 4). Shannon (1931) and Christophers (1960) also noticed that A. aegypti (L) larvae moved considerably faster than the larvae of most other species of mosquitoes. Fourth instar larvae of A. aegypti larvae can consume charcoal particles faster than 4th instar C. inornata larvae. When activated charcoal was placed in a container with 3 A. aegypti larvae and in another container with 3 C. inornata larvae (all 4th instar), the guts of the former were filled in from one hour and thirty minutes to one hour and forty-five minutes, whereas the guts of the latter species were

filled after three hours and thirty minutes. Larvae of all the species observed moved faster and more frequently when they were stimulated to activity by other organisms (Daphnia, Cyclops, etc.).

In the intervals when the brushes are not rhythmically beating to create either a feeding current or a current by which the larva moves to another position, they remain extended and separated into rows, usually four or five layers (Fig. 17), or they are retracted (Fig. 18). Figures 17 and 18 show the positions of the labral brush tormae and the epipharynx in extended and retracted positions respectively. Particles which have been brought close to the mouth by the current continue streaming towards the mouth through the spaces between the rows of hairs, or if the brushes are retracted the particles come to rest on the maxillary brushes. If the brushes are extended the particles stream into the mouth and some settle on the hairs of the pharynx, the mandibles, the maxillae and the prementum. The separation of the labral brush hairs into several rows as shown in Fig. 17 is possible because of the basal structure of the brush. Each row of hairs can move about the axis of its rod (see section 2.3.2. Fig. 4). Several rows can move in one direction together, and thus water can flow through the spaces between these groups of hairs. It also seems that the water currents can force the labral brushes to close (see section 2.3.2.). The muscles which insert on the tormal apodemes (Fig. 4) extend the brushes by contraction. This can be demonstrated in preserved specimens. The contraction of these muscles and of the epipharyngeal muscles was observed in living larvae of a filter

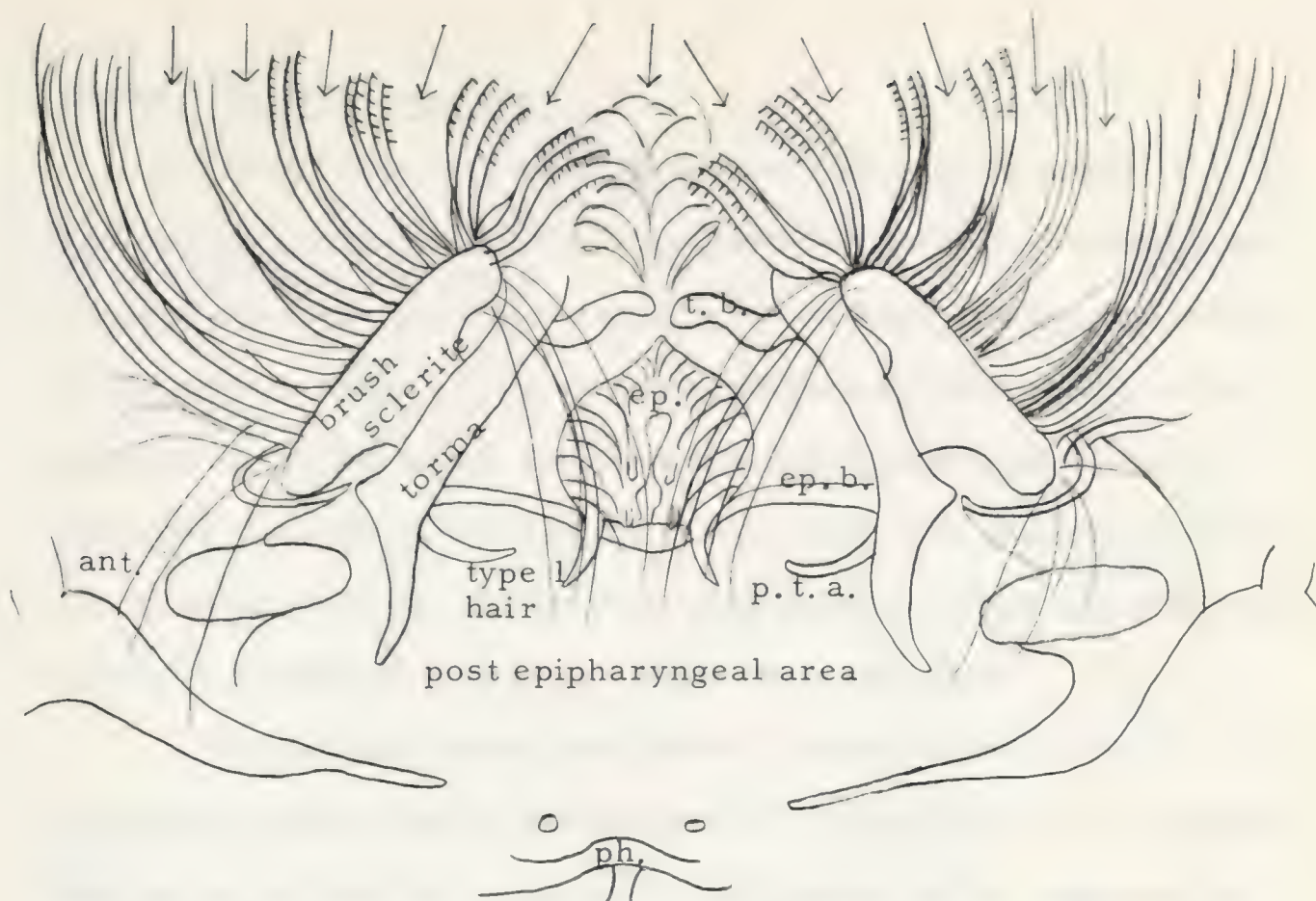


Fig 17. Ventral view of the labral area^{of} *Aedes fitchii* larva. Position of stationary labral brush hairs, extended while water of the feeding current passes towards the mouth opening. Arrows indicate the directions of water flow.

0.5 mm.

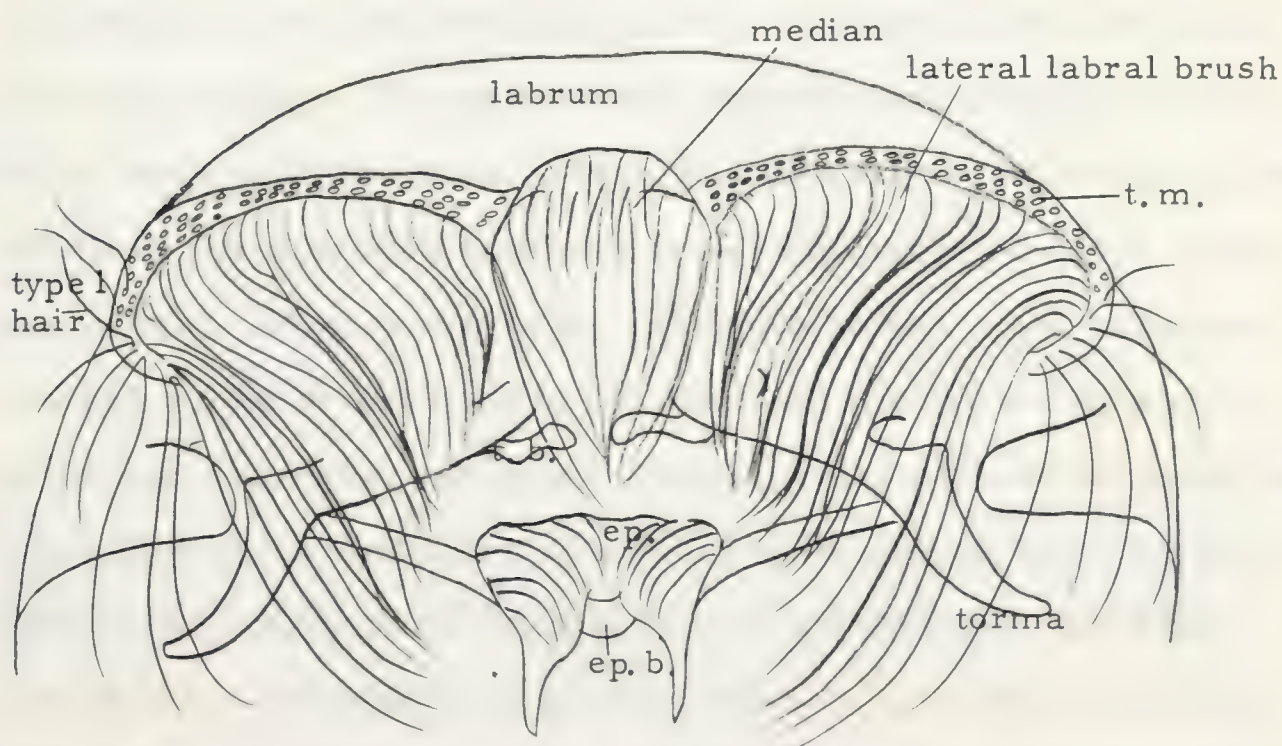


Fig. 18. The labrum of a browsing larva showing the position of the tormae and the epipharynx when the labral brushes are retracted.

feeder, Culiseta morsitans.

The feeding current of Aedes and Culiseta browsers is fast and can carry comparatively large particles as well as small ones, of an organic nature up to Objects/about one third the size of a larval head can be circulated in the stream (Fig. 19), the current and the particles reach as far posteriorly as the fourth and fifth abdominal segments and about the same distance in front of the larva. Such circulation of particles can be observed when the larva is suspended in water and also when it lies on its dorsal side in an observation spot plate.

When a larva feeds just above a loose sediment (Fig. 20) or browses its way forward through debris in a container, the particles that do not go into the mouth fall to the bottom of the container or cling to the brushes; they do not return to the feeding current. There is no room for these particles to go into the current as there is in situations where space for the current is available below the larva (Fig. 19). In the former instance the feeding current is effective only in front of the larva, and it is slowed down posteriorly of the larval head. The water flows ventrally rather than posteriorly below the body of the larva. When the larva leaves the browsing area its labral and maxillary brushes are left with many particles clinging to them, since what does not fall to the bottom of the container remains on the brushes. It is possible that some filtering is done by the labral brushes, as many of the particles that are found on them, especially on the median serrated ends of the lateral brush hairs are quite large. Since particles only slightly smaller than these have been found in the pharynx and in the intestine, and since most food seems to come into the mouth via the labral brush current, it seems

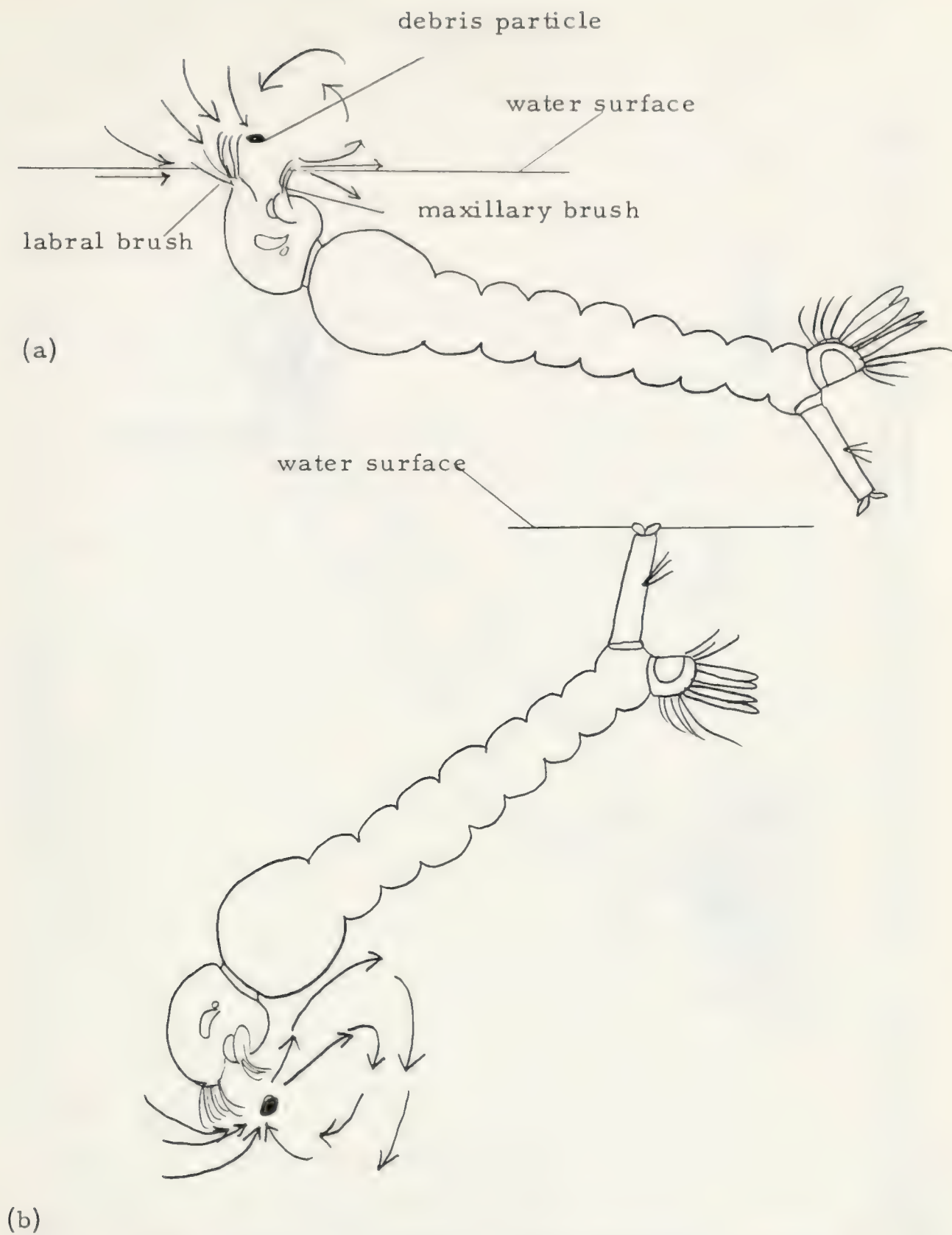


Fig. 19. Movements of particles in labral brush currents of browsing larvae. Arrows indicate direction of movement. (a) Interfacial surface feeding current (b) Current produced under the water surface.

water surface

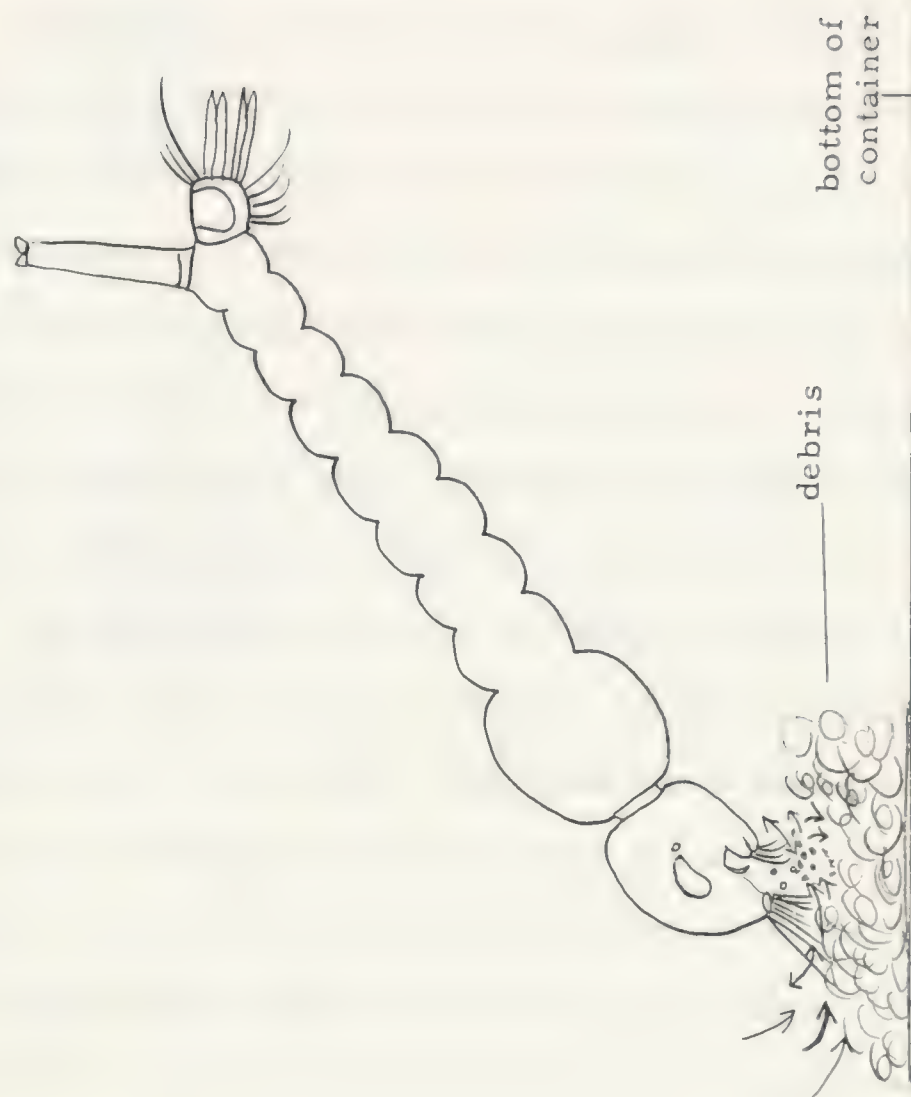


Fig. 20. A browsing larva feeding on debris particles. Double pointed arrows indicate movement of mouth brushes; single pointed arrows indicate movement of particles in the feeding current.

reasonable to assume that the particles which passed into the mouth, and eventually into the gut were filtered out by the brushes. The serrated brush hairs are useful in browsing, for as they move along surfaces they detach particles from these, and many of these particles are consumed.

Browsing is common to all the Aedes and most of the Culiseta larvae that were observed in these investigations. In ponds browsing activity was recognized, but in these instances close observation of the individual mouthparts was impossible. The larvae were simply seen moving along the bottoms of pools, along stems and leaves of immersed plants, and movements of their mouthparts were seen. Details of mouthpart movements were observed in glass containers in the laboratory.

The Aedes larva can use its labral brushes to cling to a grass stem, to the side of a container, or to the body of a pupa or another larva. (Fig. 21). While the labral brushes cling to surfaces the maxillary brushes produce a current. Since the maxillary brushes of browsers are as hard as the labral brushes and are harder than those of the filter feeders (Sec. 2), presumably the browser's maxillary brushes can create currents as well as the labral brushes. This was observed in fourth instar larvae of the following species: Aedes canadensis (Theob.), Aedes cata-
phylla Dyar, A. communis (De G.), A. fitchii (F. & Y.), A. punctor (Kirby), A. riparius (D. & K.), A. sticticus (Meigen), Culiseta inor-
nata (Will.), and Culiseta impatiens (Walker). The larvae can also browse on parts of their own body, especially on the posterior regions of the abdomen. This was observed particularly in containers

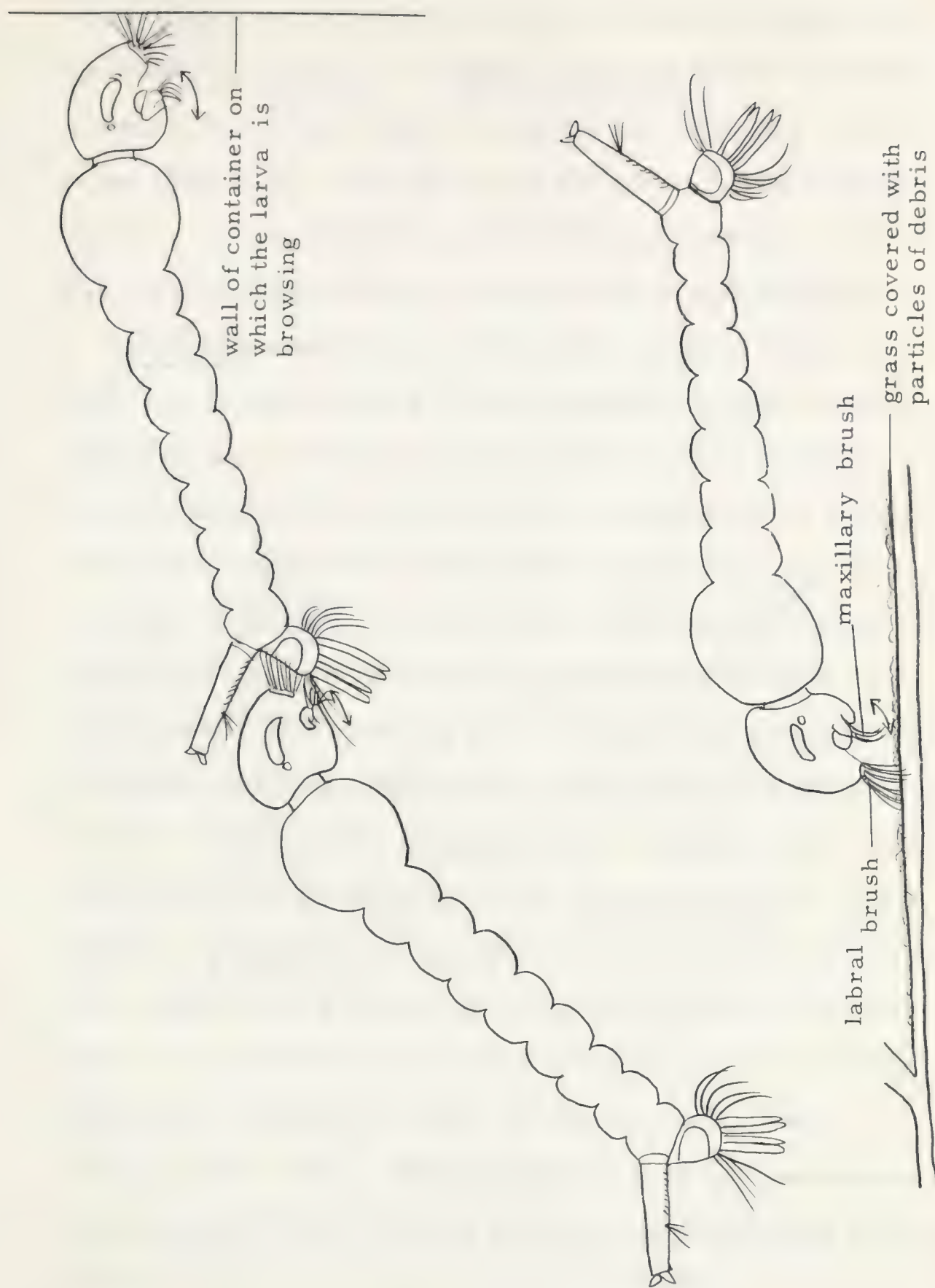


Fig. 21. Browsing larvae in various positions. Arrows indicate directions of mouth brush movements.

where Aedes and Culiseta larvae were crowded. Many times, especially C. inornata and Aedes canadensis larvae were seen browsing on the tips of their abdomens and creating a current at the same time. Thus the larvae were in loop-like positions and were moving in spiral paths on the water surface. This was particularly noticeable in the laboratory with the larvae of A. canadensis when one day in June 1960 between twenty to thirty larvae were turning in this manner for several minutes, individual larvae turning for as long as five to six minutes. Christophers (1960) states that larvae browse on parts of their own bodies, especially on the posterior parts when they are starving. This seems credible, for in situations where the circular turning and "tail" browsing was observed little food was present. This browsing at the surface is here considered as interfacial surface feeding (Fig. 19(a)) which is a common method of feeding in the Anopheles filter feeding larvae. Third and fourth instar C. inornata (Will), Aedes aegypti (L), Aedes fitchii, A. punctor, and A. riparius larvae were also seen browsing at the water surface without browsing their siphons at the same time. In this second type of filter feeding only the head of the larva was at the water surface and the rest of the body remained under water. Miall (1895) observed this phenomenon and stated that it was common among larvae which were about to pupate.

In most browsing activities all or most of the mouthparts are employed. When an object such as a long thin piece of decaying

grass comes into the feeding current, it comes in contact with the mouthparts as follows: 1. The serrated lateral labral brush hairs hold a part of it, and push the remainder posteriorly. 2. It slides over the central labral brush. 3. It passes between the epipharyngeal bristles. 4. The mandibular denticles strike it as it passes by, and if a small piece of it is thus torn it may go posteriorly with the current, it may be drawn into the mouth, or it may settle on the prementum. 5. It passes between the maxillary brushes. 6. Finally the particle of grass touches the submentum and the aulacum. During this process some of the median labral brush hairs hold the particle while the remaining hairs of the brush produce currents (Fig. 22).

It is indicated in Fig. 22 that some parts of the lateral labral brushes move only slightly whereas mostly the hairs of their more posterior parts move more actively. More commonly, however, the hairs on the brushes move simultaneously when producing a current. When a larva comes to a stop after moving about in a container, it will extend or contract the brushes gradually.

Most of the observations on the coordination of moving mouthparts were on A. aegypti and A. fitchii larvae which had been slowed down in a twenty to thirty per cent solution of methocel of 400 centipoisses. The larvae were watched in white porcelain spot plates with their ventral sides ^{turned up}. The following combinations of mouthparts were observed in action: 1. The lateral labral brushes moved in their usual antero-posterior oblique direction, and the long apical setae of both maxillae also moved backwards and forwards at the same time. 2. The lateral brushes moved in their usual direction while the setae of one maxilla remained stationary, directed posteriorly, and the setae of the other

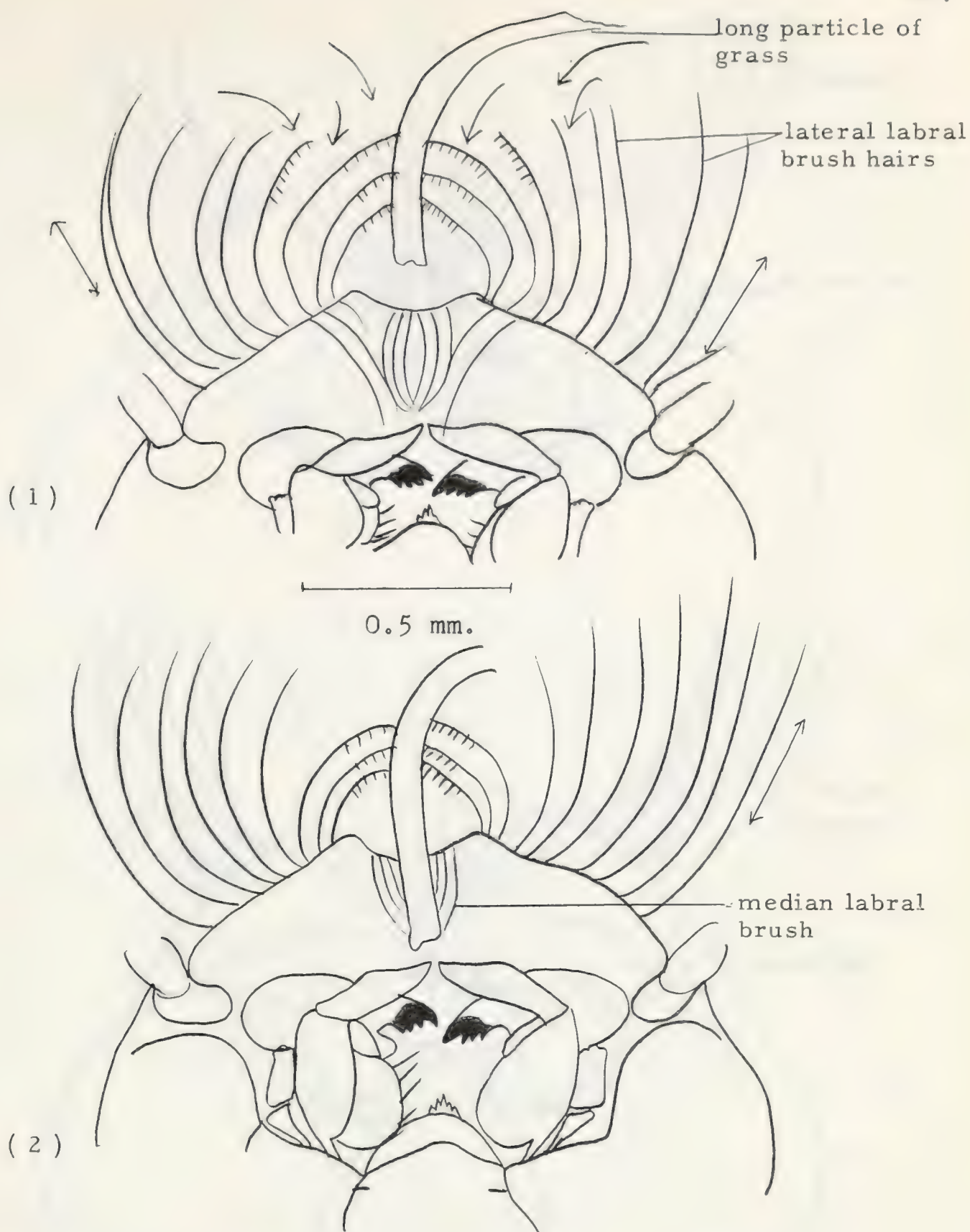


Fig. 22. Progress of a long particle between the mouthparts of a browsing mosquito larva. (1) The particle is held by the serrated lateral labral brush hairs; (2) it passes over the median labral brush; and (3) between the epipharyngeal bristles. (4) The particle is struck by the mandibles; (5) it passes between the maxillae; and (6) over the submentum and the aulacum. Single pointed arrows indicate the direction of the water current created by the lateral labral brushes. Double pointed arrows indicate the direction of movement of these brushes.

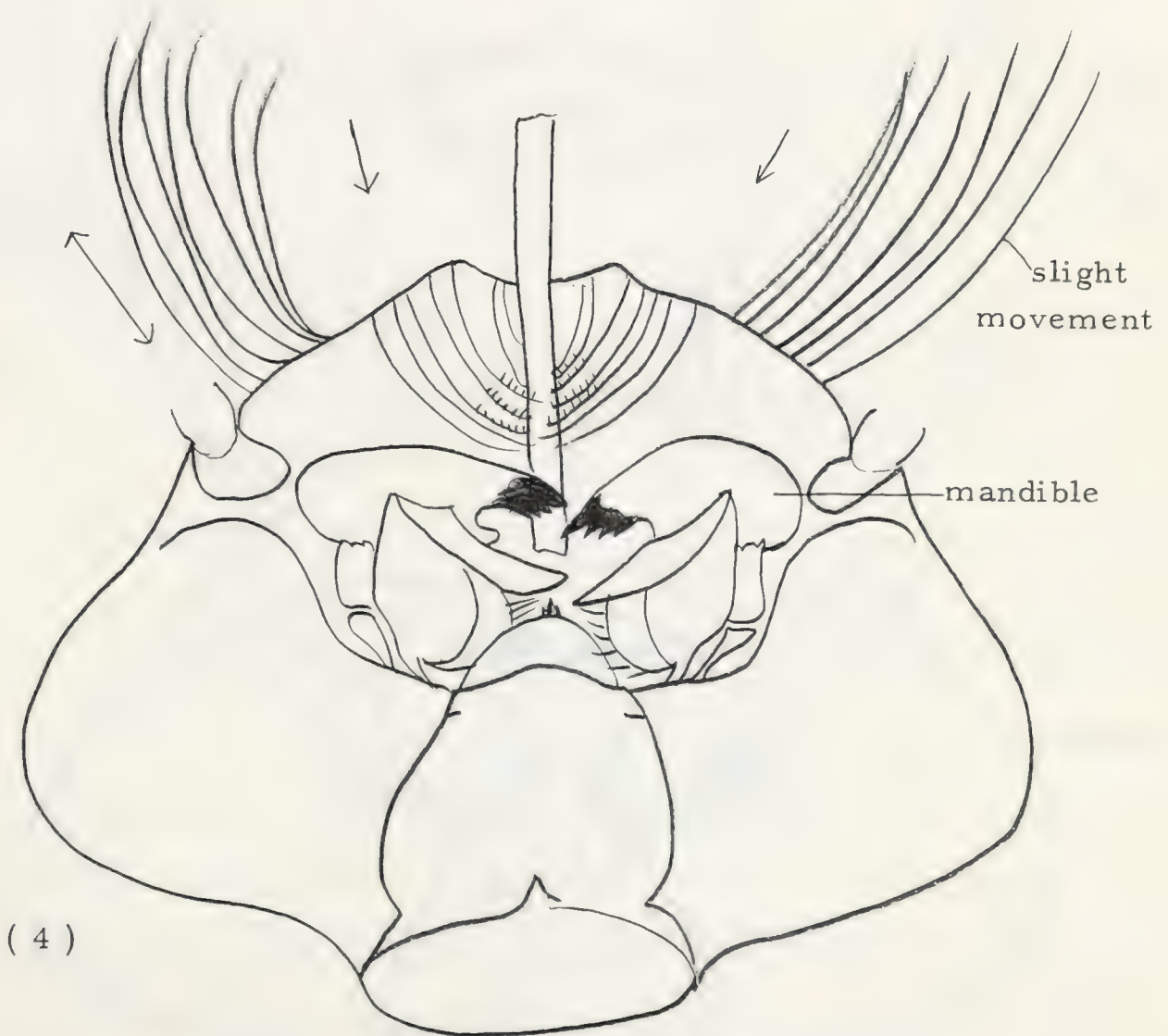
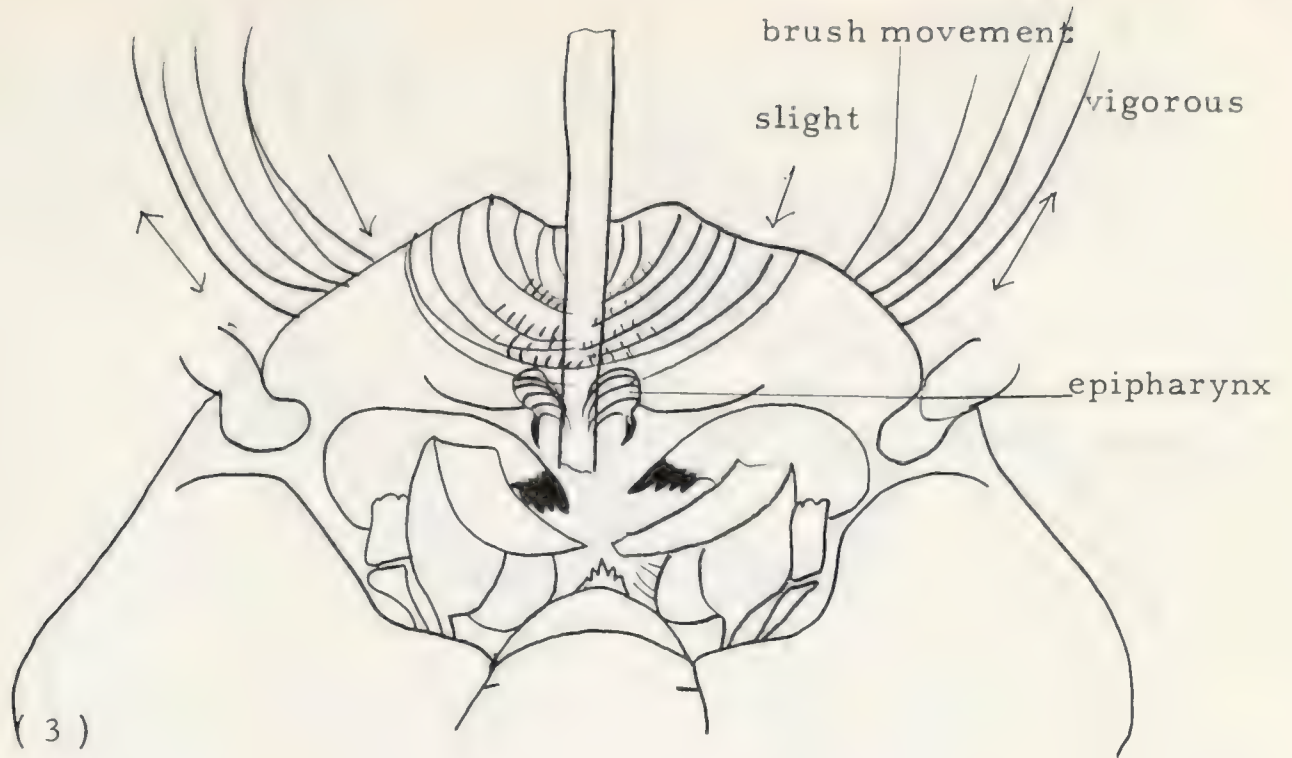


Fig. 22 . continued

0.5mm.

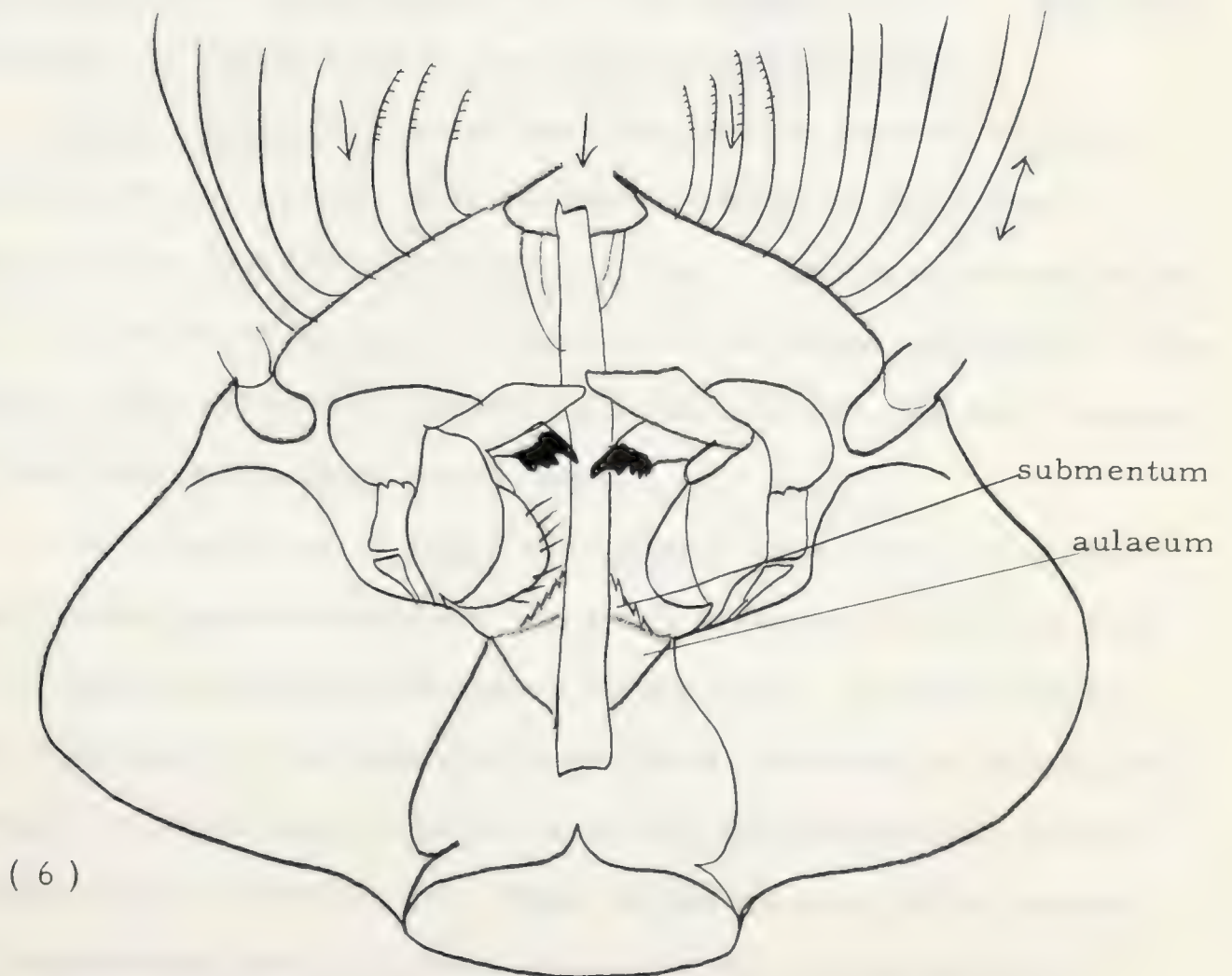
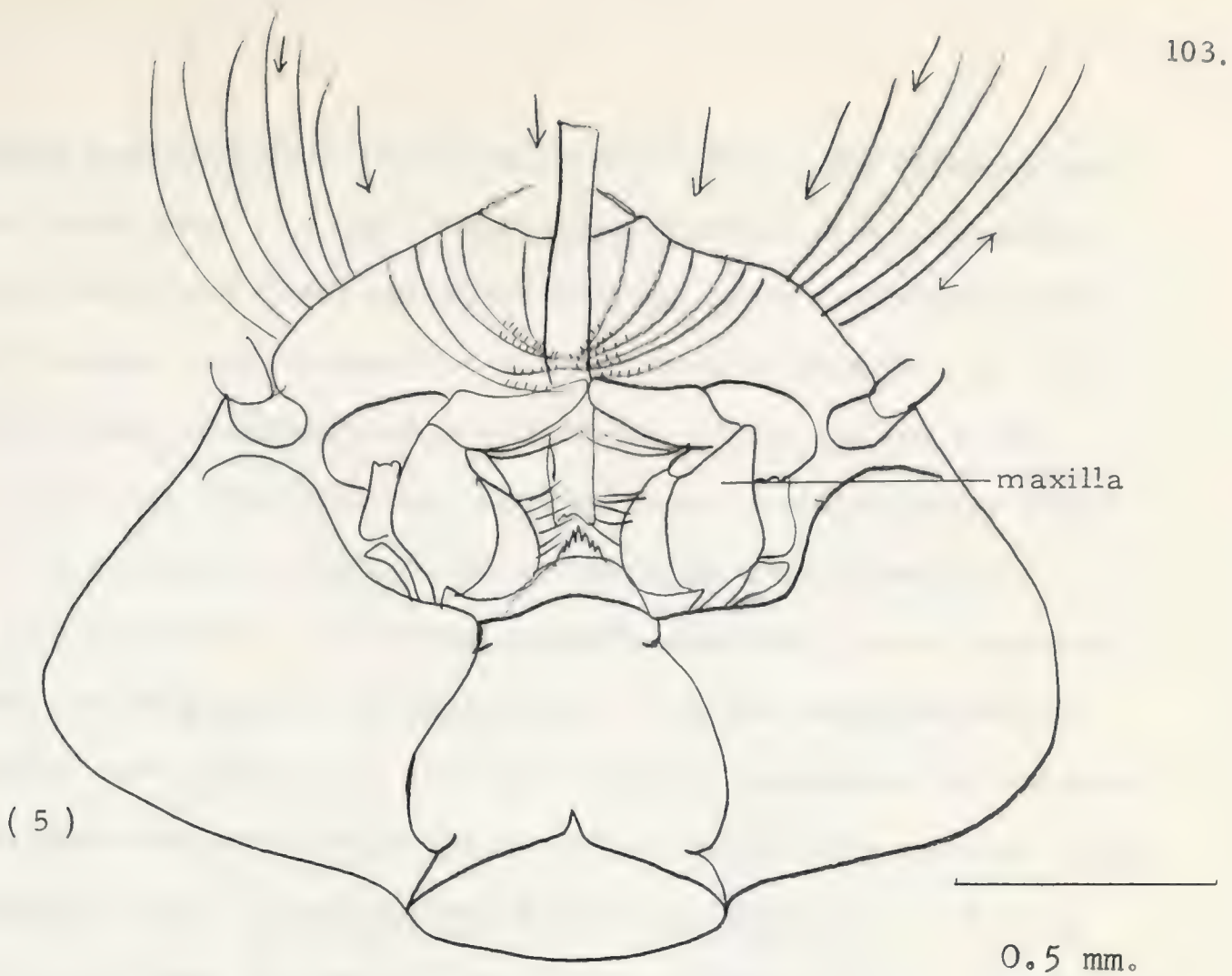


Fig. 22. continued

maxilla continued their antero-posterior motion. The epipharyngeal bars moved also. 3. The lateral labral brushes were motionless. At the same time either one of the maxillae or both maxillae waved their brushes and thus kept the 'eddy current' in motion. 4. The lateral labral brushes came to rest on the epipharynx and at the same time the other mouthparts moved in one of the following ways:

- (a.) both maxillae or one maxilla moved in the transverse plane.
 - (b.) both mandibles, or only one mandible moved in a wide horizontal plane, striking against the hypopharynx.
 - (c.) one mandible and one maxilla moved (Fig. 23).
- The same type of combination of mouthpart movements was observed in the larvae of the following species: Aedes cataphylla Dyar, A. excrucians (Walker), A. fitchii (F. & Y.), A. hexodontus Dyar, A. punctor (Kirby), A. riparius D. & K., A. sticticus (Meigen), A. vexans Meigen, and Culiseta inornata (Will.).

Aedes aegypti (L.) larvae were also seen to browse on poplar leaves in the laboratory. For two weeks ten larvae were given no other food but dried leaves of Ulnus sp. and no mortality occurred. At the end of the two week period all the larvae had pupated. The larvae of this species are also reared on leaves of a species of poplar in South Africa (Hocking, pers. comm.).

Browsing larvae of Aedes and Culiseta were observed in deep water pools (approximately one and a half to two and a half feet deep) and in shallow pools (four to twelve inches deep). In shallow pools with clear water it was possible to see larvae browsing on submerged rotting leaves and other objects for as long as three minutes without coming to the surface for air. When the larvae came to the surface they sometimes remained there for one to five minutes and they

Fig. 23. Combinations of movements of mouthparts of an Aedes fitchii (F. & Y.) larva while feeding. Double pointed arrows indicate moving mouthparts. Single pointed arrows indicate stationary mouthparts.

(1) Moving: both lateral labral brushes; brushes of both maxillae.

Motionless: mandibles, resting on hypopharynx.

(2) Moving: both lateral labral brushes; brushes of one maxilla.

Motionless: brush of right maxilla; mandibles open.

(3) Moving: brushes of both maxillae, or of only one.

Motionless: mandibles; labral brushes which are extended.

(4 a) Moving: both maxillae or one maxilla in the transverse plane.

Motionless: lateral labral brushes which are resting on epipharynx.

(4 b) Moving: both mandibles or only one mandible in horizontal plane.

Motionless: lateral labral brushes.

(4 c) Moving: one mandible and one maxilla.

Motionless: labral brushes which are retracted.

labral brushes:

106.

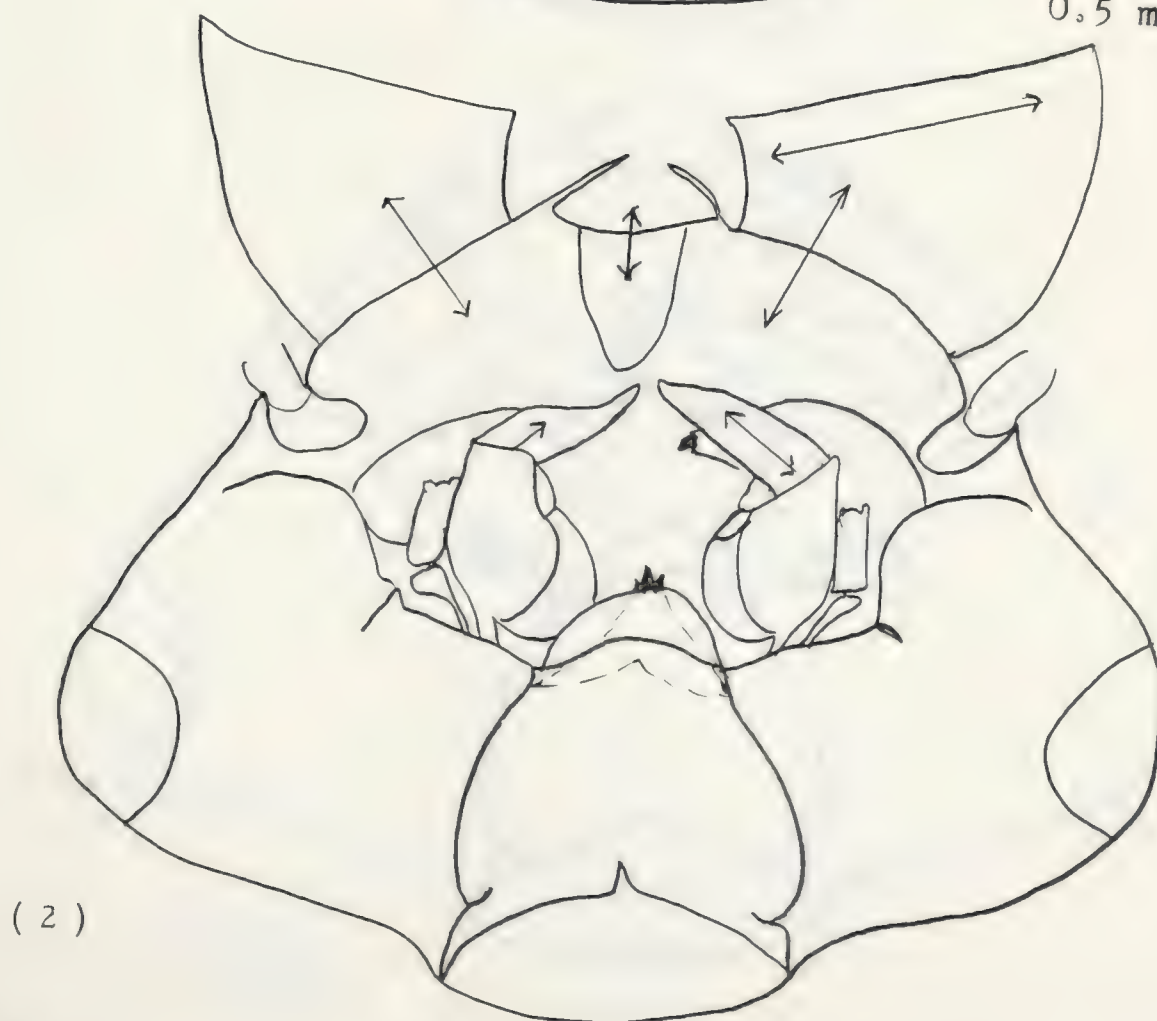
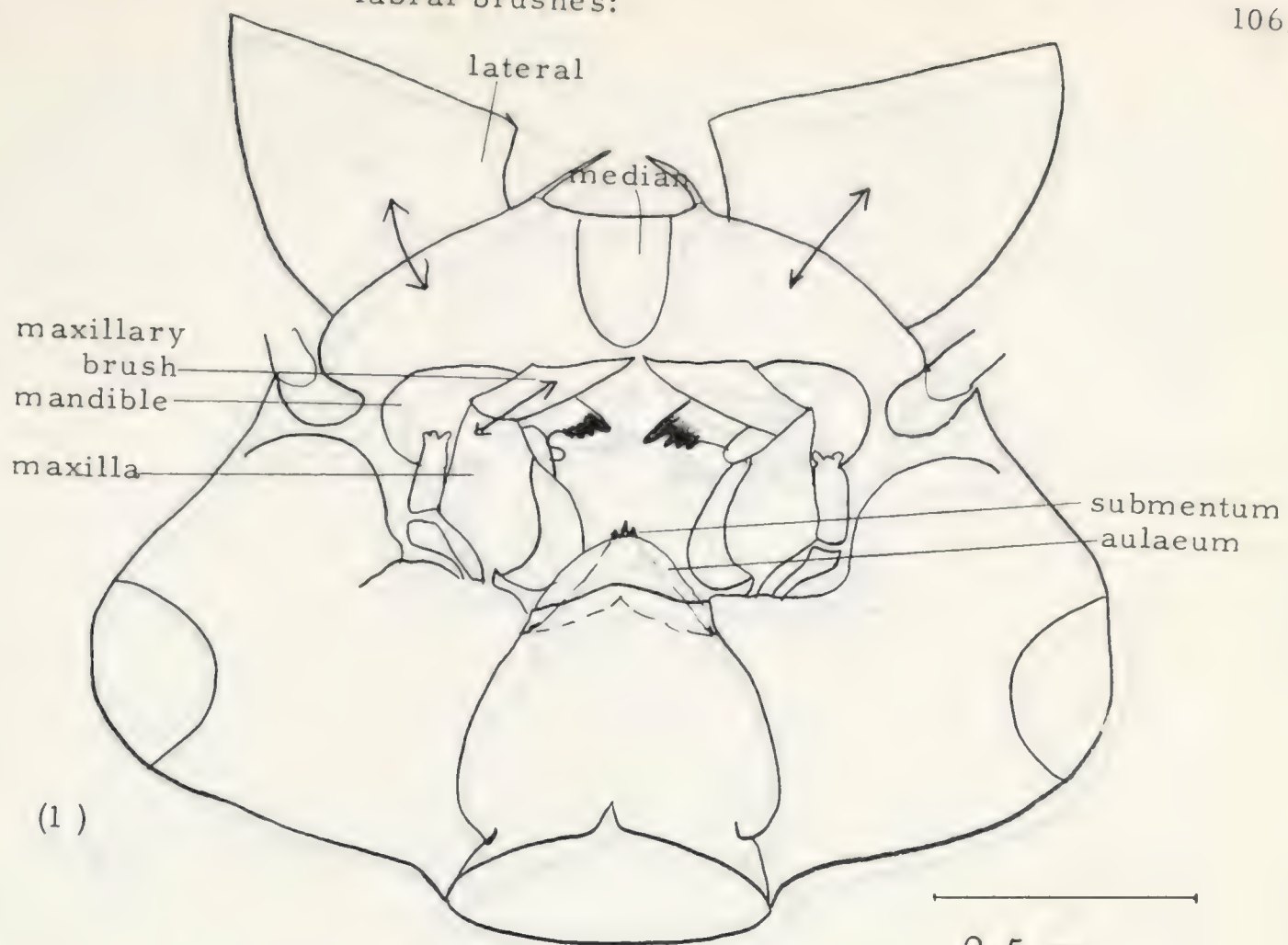


Fig. 23.



(3)



(4 a)

Fig. 23. continued



Fig. 23. continued

either moved slowly or continued to stay in one position before submerging again. Sometimes the wind disturbed the pool water surface, and some of the larvae that were at the surface moved with the wind, and some attempted to "swim" against the water current. In situations of this type, however, most larvae went to the edge of the pool where a stable resting position was found.

Several observations of larval activity were taken from a pool one and a half to two feet deep, and the courses of larval movement were recorded (Fig. 24). In this figure the movements of Aedes excrucians (Walker) and Culiseta inornata (Will.) are represented. These larvae were able to remain in a stationary position at the surface from a few seconds to four minutes. During this time they probably produced currents with their mouthparts as did the larvae of these and other browsers when observed in a glass container in the laboratory. The approximate mean distance that any one larva covered in this time (four minutes) was between four and five feet before it submerged. In a larger pool some larvae covered more space than this before submerging. The larvae submerged either of their own accord, or when they came in contact with another floating or moving object or animal in the water, such as a snail, a water beetle, a crustacean, or a dead insect floating on the surface of the water. When larvae submerged without coming in contact with something first, after detaching their siphons from the surface film, they were pulled downward by the currents of their mouthparts.

In pools populated with browsing larvae and located in areas which were partly shaded and partly in the sun, the shaded areas were much more crowded with resting larvae, although the sunny areas were used for moving about and browsing by a few larvae.

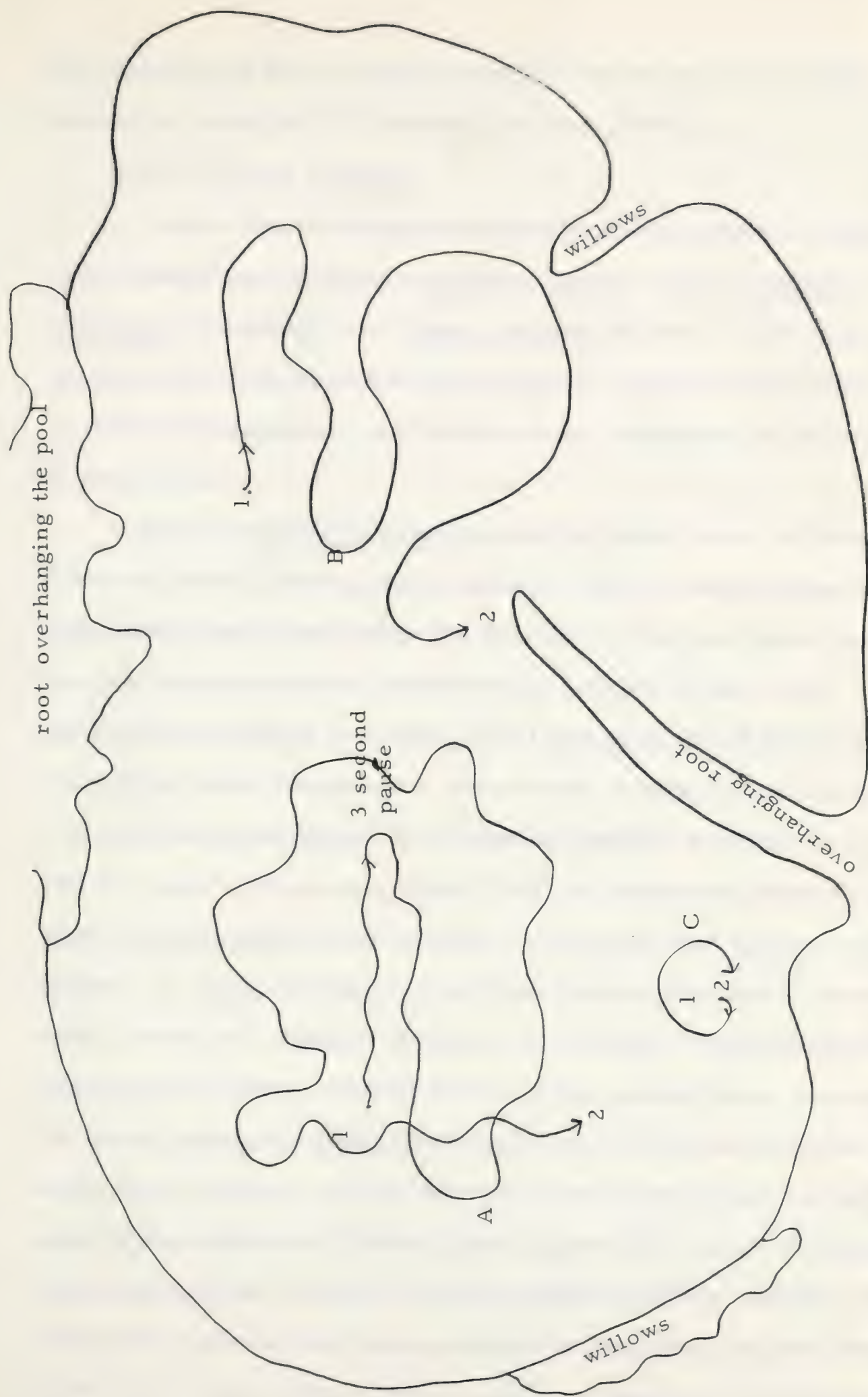


Fig. 24. Movement paths of three browsing larvae (A, B, and C) in a pool. 1. Starting point of each larva at the beginning of observation. 2. Point where each larva submerged. Arrows indicate direction of movement.

This behavior of the mosquito larvae can be interpreted as orthokinesis as described by Fraenkel and Gunn (1960).

3.3.2. Filter Feeders.

Three filter feeding species are at present known in Alberta, representing three genera; Anopheles earlei Vargas, Culiseta morsitans (Theobald), and Culex territans Walker. All of these species are rather scarce in this province, hence it was not possible to study the morphology and function of the mouthparts of their larvae in much detail.

Several Anopheles earlei larvae and adults were collected in Flatbush, Alberta during the summer of 1960. Feeding larvae of this species were observed in the laboratory, but most were reared into adults and none were preserved for morphological study. The jar rearing method of Tremblay (1955) was used, but if second or early third instar larvae were collected for rearing they did not survive until the pupal stage. It is possible that lack of oxygen in the jars was the cause of death, for Bates (1949) and Muirhead-Thomson (1951) state that Anopheles larvae require more oxygen than Aedes or Culex larvae. A. earlei larvae are small and are usually found in deep water, hence it is difficult to observe the action of their mouthparts in their natural habitat. Several larvae of this species were observed in the laboratory in circular glass containers. All the larvae were usually at the water surface. It was common to see some larvae resting with parts of the abdomen or thorax or both against the side of the container, while other larvae moved in circular paths around the container. Often two or three larvae were seen moving side by side in one direction, while one or more other larvae moved in an opposite direction (Fig. 25).

Sometimes two larvae, moving towards each other, would collide, and after colliding they both moved together in the direction initially travelled by one or the other larva (Fig. 25). It is not known what determined the final direction of movement; perhaps the larva producing the stronger current overrides the other. While moving in the various directions by means of an interfacial current the Anopheles larvae often turned their heads through 180 degrees (to the water surface) so that the ventral side of the head was at the surface, facing the observer dorsally, for longer periods of time (25 to 30 seconds at a time) than the dorsal side (approximately at 10 second intervals). From this I infer that possibly more food is gathered when the mouth is at the water surface (ventral side towards the observer) than when it is turned towards the substratum.

Observations on the larvae of Culex territans and Culiseta morsitans revealed much similarity in the movements and feeding behavior of the two species. They are found in the same type of habitat, and the mouthparts are similar in form. Since the labral brushes in these species are longer than in the Aedes or Culiseta browsers, the currents they create cover a larger area than do those of the browsers. Also these filter feeders tend to extend their labral brushes mainly laterally, whereas the browsers extend their brushes mainly antero-laterally. Several Culiseta morsitans larvae were observed in a glass jar in the laboratory. They moved rapidly by means of the labral currents, and fed at the same time; the pharyngeal movements could be seen through the head cuticle. Sometimes minute crustaceans were brought into the vicinity of the mouth with the current, but they were not consumed.

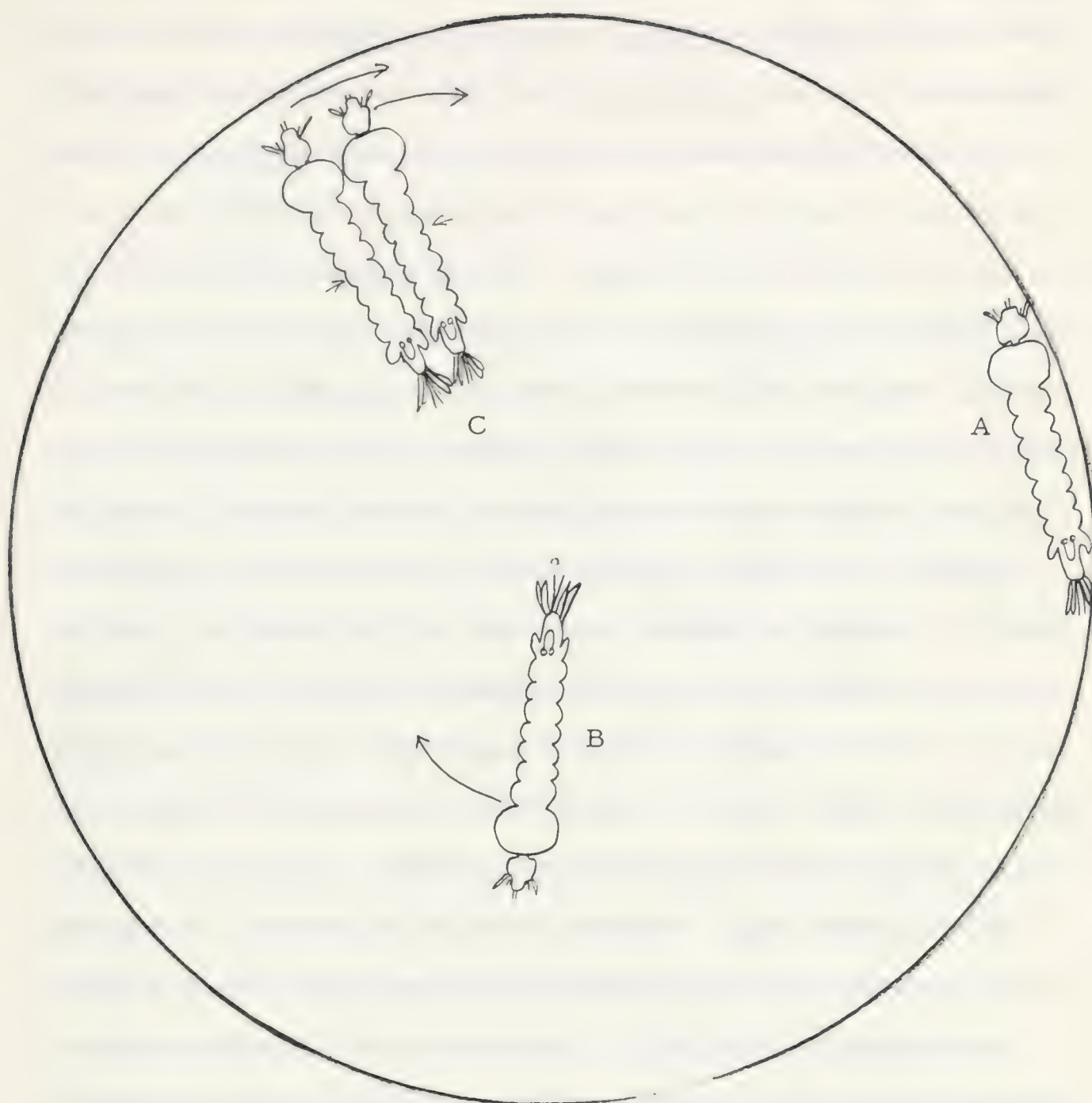


Fig. 25. Paths of movement of *Anopheles earlei* Vargas larvae in a jar. A - stationary larva, B - moving larva, C - two larvae after colliding moving in a clockwise direction. Arrows indicate directions of movement.

The food of the larvae consisted mainly of moss particles which floated in the pool water in the jar, and many that were settled on the bottom of the jar. The particles on the bottom of the jar were agitated by browsing Aedes cinereus or Culiseta inornata larvae which had been often collected with the C. morsitans larvae. Occasionally the C. morsitans were seen moving with their labral brushes just above the sedimented particles on the floor of the jar in the same manner as the browsing species. Sometimes two, three, or more of these filter feeding larvae were seen resting in one location close to each other, clinging to the water surface film with their siphons, and moving their labral brushes. Most frequently the larvae stayed in such a position between two and three minutes without being disturbed by a moving larva or some moving crustacean. When disturbed, the larvae had two alternative courses of action; 1. to submerge, or 2. to move horizontally on the water surface to another location. The first course was followed by about two thirds of the larvae and the second by the remainder of them. After submerging, each larva went in a different direction and stayed under the water surface for between ten to fifteen seconds. Upon coming to the surface the larvae either resumed their stationary positions for two to three minutes or until disturbed, or they moved horizontally, propelling themselves by the feeding current. In submerging when disturbed and in returning to the water surface the wriggling motion of the abdomen was used, this manner of motion being the same as that employed by Aedes communis larvae (Hocking 1953), A. aegypti (Christophers 1960) and other Albertan species of Aedes as mentioned here in previous pages.

In the laboratory the C. morsitans larvae showed preference for a shady portion of a container rather than the sunny part of the same container. This observation is also in agreement with the observation of Hocking (1953) on A. communis. The pools in which Culiseta morsitans and Culex territans were collected were in such positions where both sun and shade were present during some part, or parts of the day.

3.3.3. Predators

Three species of predatory larvae, Chaoborus americanus (Johannsen) Mochlonyx velutinus (Ruthe), and Eucorethra underwoodi Underwood have been collected near Flatbush, Alberta during the summers 1960 and 1961. C. americanus (Johannsen) seems closely related to the European C. crystallinus (De G.) (James and Smith 1958). C. americanus larvae were abundant both in 1960 and 1961, and they were observed feeding on the larvae of several species of Aedes in the laboratory. The feeding behavior of this species was not studied in detail, as this had been previously done by Montchadsky (1945) on Chaoborus crystallinus (De G.) and by Schremmer (1950) on Chaoborus obscuripes. Both of these authors discuss the modification of the larval mouthparts for their predatory function. The mandibles in the larvae of the genus Chaoborus are the important movable mouthparts. The maxillae are tightly connected to the ventral part of the cranium, and the prementum is reduced to a wedge-like plate. The mandibles of Chaoborus larvae do not have a primarily crushing function, but their sharp strongly chitinized teeth have a holding and pushing function (Schremmer 1950). These larvae also use their prehensile antennae for catching prey. They devour

their prey whole. Fig. 16 shows the main lines of action of the antennae and mandibles of Chaoborus americanus larva. The posterior occipital parts of the head capsule of the Chaoborus larvae are connected to the subgena by membranes (Cook 1956); this permits the mouth opening to become enlarged whenever necessary.

In Mochlonyx velutinus larva the ventral part of the head is sclerotized, but a large mouth opening is present, as the head capsule is wider than in Chaoborus. Cannibalism was observed among the M. velutinus (Ruthe) larvae when they were kept in a jar in the laboratory. The raptorial function of the mandibles^{and antennae} was observed when the larvae were catching their prey which was caught tail first. Then while the prey seemed to be held by the maxillae the mandibles continued striking it and thus pushing it further into the mouth. The process of ingestion lasted approximately two hours in the specimens that I observed. However, even three hours can elapse before the prey is digested (Montchadsky 1945). Sometimes a feeding larva lost its prey if it was disturbed by other larvae or some other organisms. Sometimes the prey was half ingested when it was lost. James (1957) observed that M. velutinus larvae are occasional predators of other mosquito larvae. A similar habit was observed in M. culiciformis De G. by Montchadsky (1953), and Montchadsky and Berzina (1959). Cannibalism was also observed in Cryophila lapponica Mart. by Montchadsky in 1953.

Eucorethra underwoodi Underwood larvae were not observed in their feeding activities, as whenever they were observed in pond water in the laboratory they were inactive for long periods of time.

The two fourth instar larvae that were observed in the summer of 1961 often remained in one location in the container for ten minutes without moving. These larvae did not survive very long in the laboratory; they may have suffered from lack of oxygen.

3.3.4. Conclusions and Discussion

The larvae that were studied in these investigations can be classified as filter feeders, browsers, and predators. Among the filter feeders and browsers more similarities are present in the structure and in the function of the various mouthparts than between either one of these types and the predators.

In the filter feeding and browsing larvae the labral brushes are used for bringing food to the larvae by means of currents which they produce by their vibrations. This phenomenon has been observed by numerous observers, dating as far back as Hooke(1665). By means of these vibrations the larvae move through the water. This method of movement is a more economical use of energy than the vigorous wriggling activity of the larvae which appears to be mainly an escape reaction (Hocking 1953a). The labral brushes of the predatory larvae are greatly reduced and are not used for producing currents. Among the browsers the labral brushes move at different rates, and also larvae of some species are generally more active than the larvae of other species (see Tables 4 and 5).

The epipharynx of the browsing and filter feeding larvae is believed to have the function of covering the mouth opening (Schremmer 1950). This was not observed in the larvae that were studied in this project. The epipharyngeal hairs were seen erected by the muscle

which moves the epipharyngeal bar, and when these hairs came in contact with the labral brush hairs, food from the brush hairs was left on them. The epipharyngeal hairs were in turn scraped by the mandibular hairs, and this food was thus passed towards the mouth opening. If the food did not go into the mouth, as often happened, particles of it remained on the prementum and on the hairs of the lacinia.

Mandibles of the browsing larvae were observed in actions of biting while the larvae were browsing on surfaces. Mandibles of predators were seen grasping and pushing the captured prey into the mouth. The mandibles of the filter feeders and the browsers move in a horizontal plane, but the mandibles of the predators move in an oblique plane which is very close to being parallel to the longitudinal axis of the body.

The maxillae of the filter feeders and browsers move in the horizontal plane, but the maxillae of the predators are immovable. The maxillary brushes of the browsers have been observed to produce currents.

The antennae of the predatory larvae are modified for use as grasping organs.

4.0 LARVAL FOOD AND MOUTHPARTS

4.1. INTRODUCTION

The aim of this part of the work was to find the main constituents of food of the mosquito larvae and also to see whether a relationship exists between the particle size of the food and the dimensions of the mouthparts.

4.2. PROCEDURES

The gut contents of several species of Aedes, Culiseta, and Culex larvae were examined and measured. Also examined were the gut contents of several freshly -killed Culiseta inornata larvae that had been collected in the field. Most of these contents were dissected out and mounted in glycerine jelly, as this is a suitable preservative for plant materials (Sass 1940). Several A. fitchii and C. inornata larvae had been fed particles of activated charcoal, and some ingested as well as some uningested particles were measured. The following head measurements were taken of the available species: head width (between the bases of the antennae), head length (between the median labral brush and the occiput), mean length of the right lateral labral brush (measured at the center of the brush), width of the right lateral labral brush (measured the length of the sclerite at the base of the brush), and the width of the epipharyngeal constriction (width between the most posterior, longest teeth of the epipharynx).

An analysis was made of the material suspended in ten liters of water which was taken from a pool near Edmonton where C. inornata larvae were collected in September , 1961. This water was passed through six sieves of different sizes, and some particles that passed through were measured. Material that did not go through the sieves

was examined, and a rough estimate of its composition was made. This material was then dried until a constant dry weight was obtained; it was ashed in a muffler oven at 575°C ; the ash was weighed; and the percentage loss was calculated.

4.3. OBSERVATIONS

Table 6 contains a summary of the sizes of particles that were found in the gut contents and in the environment of the larvae of Aedes fitchii, Culiseta inornata, and Culex territans. Table 7 contains a list of particles that were identified from the guts of fourth instar larvae of these species. From this table it is seen that the gut contents in the three species were similar to each other. The guts of a few Chaoborus americanus larvae that were examined were filled with muscle tissues; probably these were body tissues of other larvae.

The relationship between the structure of some mouthparts and the feeding habits of larvae is shown in Fig. 26. The points on the graph were derived in the following manner: 1. for the position on the horizontal axis the mean length of the right labral brush was multiplied by its width to give the area through which the brush moved. This product was divided by the product of the head length and the head width. 2. for the position on the vertical axis the width of the epipharyngeal constriction was divided by the head width. Each point represents the mean value for a species. The species represented on the graph, the number of larvae measured, as well as the mean values of the dimensions of the labral brushes and the epipharyngeal constriction are listed in Table 8. Also indicated in this Table is the division of the larvae studied into filter feeders,

Table 6. Size ranges of some particles that were found in the gut contents and the surroundings of fourth instar mosquito larvae.

Particle size range maximum width (microns)	Browser				Browser				Filter feeder	
	<u>Aedes fitchii</u>				<u>Culiseta inornata</u>				<u>Culex territans</u>	
	charcoal	found in:	natural food		charcoal	natural food	natural food		gut	gut
	particles	gut, surroundings	gut	surroundings	gut	surroundings	gut	surroundings	gut	surroundings
Smaller than 7.5	6.1 %	4.3%*	3.1 %	**	4.0 %	4.0 %	2.7 %	**	12.0 %	**
7.5 - 9.9	10.2	7.2	7.4		8.2	5.7	9.8		35.4	
10 - 14.9	31.7	29.5	6.3		27.1	10.1	6.0		40.1	
15 - 19.9	10.0	11.1	27.2		9.1	30.3	35.6		7.2	
20 - 24.9	8.0	9.0	11.5		9.5	12.0	9.0		6.3	
25 - 29.9	9.8	13.0	9.3		12.2	11.7	10.0			
30 - 34.9	9.2	6.0	13.6		9.4	6.2	11.0			
35 - 39.9	5.6	4.9	10.1		3.9	4.0	8.5			
40 - 44.5	5.0	11.0	6.7		10.0	5.0	6.0			
45 - 71	4.0	5.0	5.3		8.0	10.0	2.0			
Total No. of particles measured	500	500	400		500	500	120		300	

* Charcoal particles of similar size range were suspended in the surroundings of both species.
 ** Food of similar particle size was found in larval habitats of all three species.

Table 7. List of particles identified from dissected intestinal contents of fourth instar larvae of

Aedes, Culex, and Culiseta. x indicates presence of a particular item.

Particles	<u>Culiseta inornata</u> (Will) Particles found in: intestine surrounding water	<u>Aedes fitchii</u> (F&Y) Particles found in intestine	<u>Culex territans</u> Walker Particles found in intestine
Diatoms			
<u>Fragilaria</u> sp.	x	x	
<u>Gomphonema</u> sp.	x	x	
<u>Navicula</u> sp.	very abundant	x	
<u>Pinnularia</u> sp.	x	x	
<u>Stauroneis</u> sp.	x	x	
Flagellates			
<u>Chlamydomonas</u> sp.	scarce		
<u>Euglena</u> sp.	present alive		
<u>Phacus</u> sp.	present alive	abundant	
Arthropod material			
Pieces of cuticle	x	x	
Culicine larval spines	x	x	
Culicine larval hairs, tufts of hair	x		x
Green Algae			
<u>Ankistrodesmus</u> sp.		x	
<u>Geminella</u> sp.	x	x	
<u>Microspora</u> sp.		abundant	
<u>Scenedesmus</u> sp.		x	
<u>Spirogyra</u> sp.	x	very abundant	x

Table 7. continued

Particles	<u>Culiseta inornata</u> (Will) Particles found in: intestine surrounding water	<u>Aedes fitchii</u> (F&Y) Particles found in intestine	<u>Culex territans</u> Walker Particles found in intestine
Blue Green Algae			
<u>Anabaena</u> sp.		x	
<u>Gleocapsa</u> sp.	x		
Fungi			
<u>Cladosporium</u> spores	x	x	
<u>Helminthosporium</u> spores			
<u>Rust - telopores</u>		x	x
- uredospores	x		
Smut spores	x	x	x
Brain Hyphae			
Imperfect Fungi	x		
Pollen of:			
pine			x
poplar	x	x	
compositae	x	x	x
Plant fibers			
xylem	x	x	x
tracheids	x	x	x

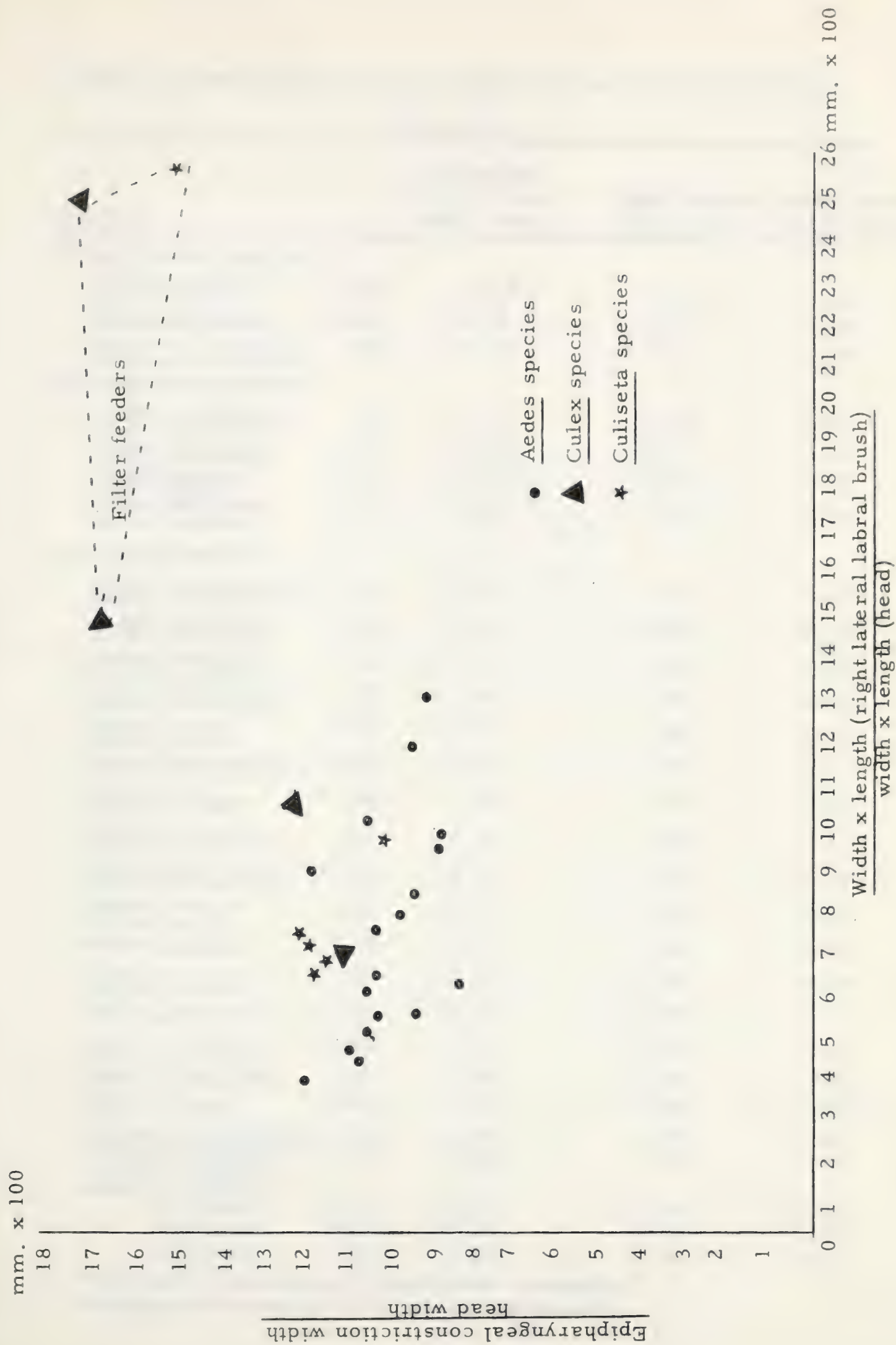


Fig. 26. Relation between feeding habits and morphology of mouthparts of mosquito larvae.

Table 8. Some dimensions of mouthparts of species with different
food habits.

Species		Epipharynx constriction width (mm.)	Right lateral labral brush length (mm.)	width (mm.)
Filter feeding species:				
<u>Culex tarsalis</u>	(18)*	0.32 [#]	1.26	0.49
<u>Culex territans</u>	(22)	0.38	1.35	0.40
<u>Culiseta morsitans</u>	(2)	0.32	1.70	0.80
Intermediate species:				
<u>Aedes canadensis</u>	(2)	0.21	0.89	0.50
<u>Aedes cinereus</u>	(1)	0.20	0.75	0.50
<u>Culex pipiens</u>	(20)	0.22	0.82	0.41
<u>Culex restuans</u>	(15)	0.20	0.69	0.40
Browsing species:				
<u>Aedes campestris</u>	(1)	0.25	0.12	0.60
<u>Aedes communis</u>	(4)	0.22	0.90	0.40
<u>Aedes dorsalis</u>	(13)	0.19	0.65	0.33
<u>Aedes excrucians</u>	(5)	0.22	0.80	0.40
<u>Aedes fitchii</u>	(17)	0.25	0.81	0.40
<u>Aedes hexodontus</u>	(17)	0.20	0.72	0.41
<u>Aedes impiger</u>	(1)	0.21	0.85	0.60
<u>Aedes intrudens</u>	(1)	0.26	0.60	0.40
<u>Aedes implicatus</u>	(20)	0.16	0.62	0.39
<u>Aedes pionips</u>	(1)	0.30	1.10	0.50
<u>Aedes punctor</u>	(15)	0.19	0.80	0.52
<u>Aedes riparius</u>	(1)	0.25	0.90	0.60
<u>Aedes spencerii</u>	(1)	0.26	0.80	0.70
<u>Aedes sticticus</u>	(5)	0.23	0.80	0.50
<u>Aedes stimulans</u>	(1)	0.25	0.80	0.39
<u>Aedes vexans</u>	(15)	0.23	0.82	0.40
<u>Culiseta impatiens</u>	(1)	0.30	0.85	0.50
<u>Culiseta incidens</u>	(1)	0.25	0.90	0.40
<u>Culiseta inornata</u>				
4th instar	(20)	0.22	0.74	0.40
3rd instar	(10)	0.16	0.59	0.26
2nd instar	(5)	0.09	0.44	0.20

* indicates the number of specimens measured.

indicates the mean value (where applicable).

browsers, and intermediates between these two types. Characteristics of the morphological intermediates are given in section 2. In Fig. 26 the intermediates are shown with the browsers.

Of the seived materials found in the pool where C. inornata larvae were collected in September of 1961, rough estimates of proportions of the various materials present were made with the following results:

Mesh No. 45:

- Approximately : 60% Cyclops (alive) and copepods.
- 20% decaying animal and plant material, including: mosquitoeggs, egg cases, beetle abdomens, mosquito wings, decaying plant material.
- 20% algae, mainly Spirogyra.

Similar estimates were made of the materials that were seived through sieves of the following mesh numbers: 60, 80, 230, and 325. From the dry and ash weights of the seived plankton the percentage of organic material was calculated as follows:

Mesh No.	45	60	80	230	325
Dry wt. (gms.)	0.0264	0.0300	0.0448	0.4340	0.1560
Ash wt. (gms.)	0.0129	0.0166	0.0328	0.3330	0.1240
Difference:	0.0135	0.0134	0.0120	0.1010	0.0320
% loss:	0.0135x100	0.0134x100	0.0120x100	0.1010x100	0.0320x100
(organic material)	0.0264	0.0300	0.0448	0.4340	0.1560
	= 50.4%	= 44.7%	= 26.8%	= 23.3%	= 20.3%

From these figures it is seen that the surroundings of the C. inornata larvae were rich in organic materials.

4.4. CONCLUSIONS AND DISCUSSION

After examining the gut contents of browsing, filter feeding, and predatory larvae it was found that the browsing Aedes and Culiseta larvae feed on foods of similar types and similar particle sizes. The following are the approximate proportions of the different size ranges of the food particles in the guts of Aedes fitchii and Culiseta inornata larvae: less than 15 microns - one-sixth, 15 to 22 microns - one third, 22 to 40 microns - one third, 40 to 60 microns - one sixth of the measured particles.

The charcoal particles that the larvae of these two species ingested were mostly between 7.5 and 15 microns, whereas particles of plants and minute animals that were ingested by the same species were between 15 and 40 microns. It is probable that some plant and animal particles before entering the mouth of a larva were folded. Also when the larvae browsed on plant surfaces they bit pieces of plants, scraped surfaces, and thus obtained particles of various sizes which their mouthparts pushed into their mouth openings. However, when charcoal particles were suspended in the water, the larvae ingested the small particles that were brought to the mouth with the feeding current, and rejected the large ones. From the proportions of the particle sizes found in the guts of larvae and in the water around them, it appears that the larvae do not discriminate on small particles, but they seem to discriminate on large ones.

As the charcoal particles did not remain in suspension in the water they were not fed to the filter feeders. Pond food from the guts of these larvae was measured (Table 6). Also measured were the

spaces between the groups of labral brush hairs through which the feeding current passes. The size range of these spaces was found to be similar to the size range of the particles in the guts. Thus filter feeding is possible among these larvae, for if the ingested particles were larger than the spaces between the hairs, they would not be trapped in the brushes, but would remain on the surface. On the other hand, very small particles would pass through the brush with the water current without becoming entangled in it. Therefore, food particle size about the same as the hair spacing seems reasonable in the larvae which are commonly called filter feeders.

Also, most of the food particles found in the guts of filter feeders were of the same order of size as the charcoal particles ingested by the browsers, and smaller than the food particles of browsers that fed in the field. Thus the browsers took in small charcoal particles by a filter feeding mechanism, and bit off large particles. Also the browsers by their browsing activities kept the charcoal particles in suspension.

According to Bates (1949), Shipitzina in 1935 found that fourth instar larvae of Anopheles messeae were able to swallow sand particles from 68 to 165 microns. If these larvae can swallow such large particles, it is possible that their mouth openings are larger than those of the culicine larvae. Size range of food particles found in the guts of three English species of Simulium larvae was found to be 1.7 to 15.1 microns by Williams et al. (1961). However, the size of the mouth openings of these larvae was not given.

From Table 7 it is seen that the browsing larvae whose guts were examined fed on plant particles and on microscopic animals, whereas the filter feeder Culex territans had fed only on plant particles. From the same table it is also seen that almost all the types of particles that were present in the pool water where the C. inornata larvae were collected were found in the intestines of larvae of the same species. It can be said then that these larvae do not discriminate in the type of food that they ingest. Other workers have come to similar conclusions: Coggeshall in 1926 as reported by Bates (1949), Howland (1930), both of whom worked with anopheline larvae, and Becker (1958) who worked with the larvae of Culicoides circumscriptus Kieff. The above mentioned authors have found algae, diatoms, and other plant particles in the guts of Anopheles and Culicoides larvae. Similar food materials have been also found in Chironomus hyperboreus (Rempel 1936), and in culicine larvae (Horsfall 1955). Living specimens of a Euglena species have been found in the gut of Anopheles maculipennis (Bekker 1938).

From Table 8 it is seen that the lateral labral brushes of the filter feeding larvae are longer than those of the browsing larvae. Therefore, when the mouthparts of the filter feeders are in a current-producing action, they should cover a greater volume of water than the labral brushes of the browsing larvae.

5.0 GENERAL CONCLUSIONS AND DISCUSSION

According to the functions of the mouthparts three types of mosquito larvae can be recognized in Alberta: filter feeders, represented by Culex territans, Culiseta morsitans; browsers, including most of the Aedes and Culiseta species; and predators, represented by species of Chaoborus, Mochlonyx, and Eucorethra. The filter feeders are characterized by labral brushes consisting of long, thin, simple hairs, lightly sclerotized mandibles, and large triangular maxillae with long thin brushes. The browsers have shorter labral brushes with some serrated, thick hairs; rectangular maxillae with shorter, thicker brushes, and moderately sclerotized mandibles. The predators bear only a few setae on their reduced labral areas and on their much more fused maxillae, and they have heavily sclerotized mandibles.

Among the browsers morphological intermediates occur. One type of intermediate, represented by Aedes canadensis and A. cinereus, has short labral brushes with simple hairs, browser-like mandibles, and maxillae similar to those of the filter feeders. The other type of intermediate, represented by Culiseta impatiens and Culiseta inornata, has typical browsing labral brushes and mandibles, but has maxillary structure closely related to that of the predators.

Not much variation was observed in the structure of the labral brushes, mandibles, or maxillae among most of the browsing Aedes larvae that were studied. However, specific differences were found in the numbers of serrations on the sclerotized plates of the prementum, and on the triangular

submentum. These characters may be taxonomically useful.

By staining with Mallory's triple stain it was found that the cuticle of the mouthparts varies in hardness and flexibility. The median hairs of the lateral labral brushes of the browsers have hard basal and central parts, and flexible parts just above the bases, and at the tips. Since the tips of the serrated hairs are soft, they detach mostly soft food particles from the surfaces on which they browse.

A correlation was found between the dimensions of the food particles found in the guts of filter feeding larvae, and the dimensions of the spaces between their labral brush hairs. It was found that the browsers are capable of filtering out particles from water. Morphological intermediates can obtain their food by filtering and browsing.

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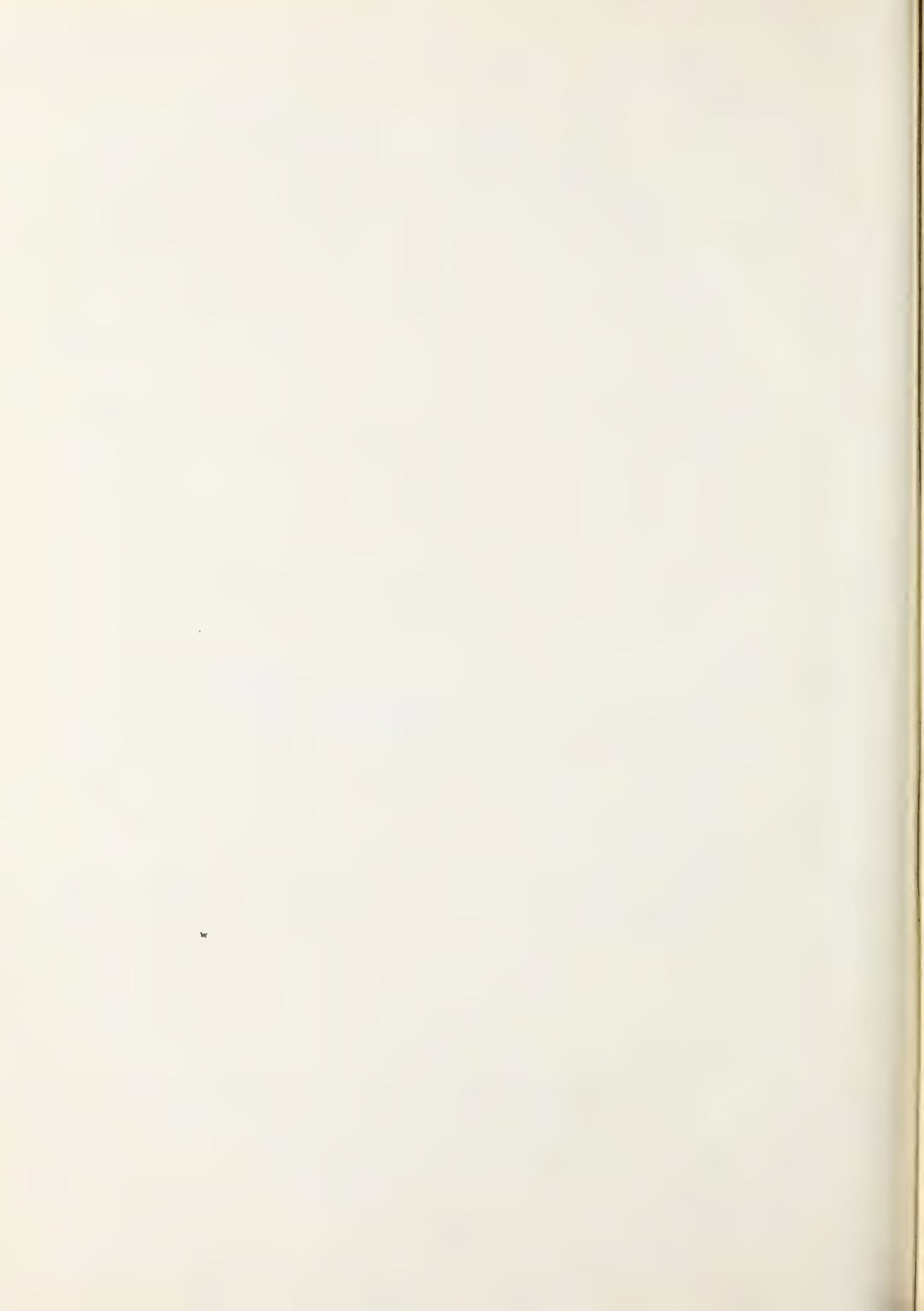
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